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THE LIFE HISTORY OF THE WHITE CRAPPIE (POMOXIS ANNULARIS) OF BUCKEYE LAKE, OHIO[1]

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INTRODUCTION

The white crappie is relatively abundant in the Great Lakes region and the upper Mississippi Valley. It is common in most of our Ohio Lakes and ponds. It flourishes in shallow muddy lakes and ponds and is easily propagated. This paper is concerned with the life history of the white crappie of Buckeye Lake, Ohio, and includes information from the fertilized egg to the adult stage. This information was obtained in the field and in the laboratory, from workers in the field, and from papers on the white crappie.

I am indebted to the Division of Wildlife of the Ohio Department of Natural Resources for making this work possible, and to the personnel of the Fish Management Division, particularly Edward Wickliff, John Pelton, Ray Riethmiller and Ray Hughes, for help in pursuing this work. I am especially indebted to Paul Chanley, Denison University-1952, now Research Biologist of the Fish and Wildlife Service of the United States Department of the Interior, for help in all phases of this work both in the field and in the laboratory.

MATERIALS AND METHODS

Fishes were collected from fyke test nets and by seining from various parts of Buckeye Lake during 1950, 1951 and 1952. Samples were removed from the nets every few days whenever the weather was favorable. The fishes were taken to the laboratory where they were measured and weighed. The body weight and ovary weight were determined, and the ratio of these weights was computed. The number of eggs per specimen was determined by counting the number in a weighed or measured sample, and then the total number of eggs was determined by multiplying by the total weight or volume of the ovary. The volumetric method was used when the eggs could be stripped easily from the mature fish.

For a study of growth at various ages the length of the fish was determined

when it was caught. Scales were removed from the region between the lateral line and the anterior end of the spiny dorsal fin. The scales were placed between two glass slides and held together with scotch tape. They were then projected on a screen by means of a rayoscope. The distances between the focus and each annulus, and between the focus and the margin of the scale were determined. Then the length of the fish at each annulus was computed by the following formula:

$$L:S::L_1 \text{ is to } S_1.$$

L equals the length of the fish when caught
S equals the distance from the focus to the margin
L_1 equals the unknown length of the fish at the time the scale was at any point S_1.

Hence $$L_1 = \frac{L \times S_1}{S}$$ Johnson (10)

Two hundred and seventy-six fishes were included in the study.

For the study of the food habits the stomachs of the fishes were removed and preserved in 10% formalin. Identification, numerical counts, and volumetric measurements were made of the stomach contents.

For the study of the embryonic development, mature fishes were stripped of their eggs and sperms by applying pressure to the sides of the abdomen. The eggs and sperms were mixed together in culture dishes in tap water at temperatures between 68 degrees and 73 degrees F. Fertilization and development were observed through the binocular microscope. Most drawings were made from living specimens. Some post larval forms were preserved, stained in paracarmine and the internal structures drawn.

DESCRIPTION OF THE SPECIES
External characters

Like all sunfishes the body of the white crappie is laterally compressed. The dorsal and anal fins are large and about equal in size. This character serves to differentiate this species from other sunfishes with the exception of the black crappie. The dorsal fin has six spiny rays, though five or even seven rays may be present. The anal fin has six spiny rays. The head is long. The mouth is wide. The profile is sinuate from the snout to the dorsal fin. Figure 1.

The white crappie is not a colorful fish. Its body is olive green in color and mottled with dark green patches. The dark pigment on the body is concentrated into several vertical bands which become indistinct on the lower sides of the body. The dorsal fin, the tail fin and the anal fin also have a mottled appearance due to the localization of the pigment into many small patches. The belly is usually light in color, while the back, from the head to the tail, is quite dark. During the breeding season the male white crappie is more deeply pigmented than the female.

POMOXIS ANNULARIS
WHITE CRAPPIE

Mouth cavity
Tongue
Gill rakers
Gill filaments
Ventral aorta
Bulbus arteriosus
Ventricle
Auricle
Liver
Pyloric caeca
Intestine
Stomach

Spleen
Anus
Ovaries
Genital opening
Ureter

Gall bladder
Kidney
Air bladder
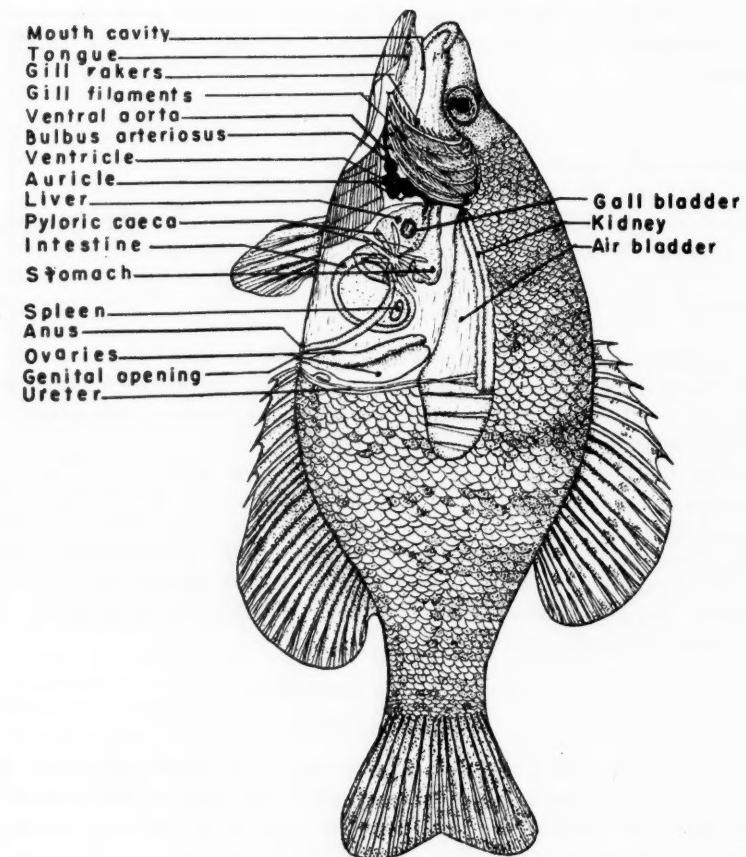
FIG. 1. Internal Anatomy

White crappies reach a length of 17 inches and a weight of 2½ pounds in some of the large reservoirs. The largest white crappie taken from Buckeye Lake in this study was 13¼ inches.

Internal characters

The floor of the mouth bears a small elevation which represents the tongue. The tongues of all fishes are poorly developed and represent only a part of the tongue of higher forms. In many fishes the tongue bears teeth. This is not true

of the white crappie. However, vomer, palatine and ectopterygoid bones of the roof of the mouth are supplied with teeth. The pharynx is supported by four pairs of gill arches. Attached to the arches are gill filaments through which the exchange of gases takes place during respiration. The lower surfaces of the arches bear many short teeth. Along the free margin of the arches there are many tiny projections called gill rakers (Fig. 1) which serve to strain the water as it passes through the gill slits. The gill rakers in the white crappie are long and slender. The pharynx opens into a short esophagus whose inner surface bears many finger-like papillae. The presence of papillae serves to differentiate the esophagus from the stomach. The inner wall of the stomach, when empty, has many longitudinal ridges called rugae. These disappear as the stomach becomes distended with food. The lower curved portion of the stomach is called the pylorus and is marked at the distal end by a circular constriction, the pyloric valve. The valve marks the end of the stomach and the beginning of the intestine. The part of the intestine adjacent to the valve is called the duodenum. Attached to its outer surface are nine fingerlike tubes, the pyloric caeca. These are evaginations of the duodenum and serve to increase the surface for the digestion and absorption of food. The reddish brown organ that surrounds the stomach is the liver. Embedded in its substance is the globular gall bladder which stores bile from the liver. During digestion bile passes from this organ into the common bile duct which opens into the duodenum.

There is no marked difference between the small and large intestines. Beginning at the duodenum both are coiled within the body cavity. The large intestine opens to the exterior at the anus which is located between the pelvic fins.

The male reproductive system consists of a pair of long pencil-like, whitish organs, the testes, and a pair of ducts, the vasa deferentia. These open to the exterior by means of a genital pore just posterior to the anus.

The female reproductive system consists of a pair of ovaries, or ovisacs, and a pair of oviducts. The latter are merely elongations of the ovisacs. The eggs are produced in the outer walls of the ovaries and never enter the body cavity as they do in Amphibians. As the eggs become mature they pass from the outer wall into the central cavity of each ovary and into the oviducts which open to the exterior by the genital pore posterior to the anus.

The kidneys are located above the air bladder. They are long narrow organs embedded in the dorsal wall of the body cavity one on each side of the backbone. Wastes are carried from these organs by ducts, the ureters, which unite to form a common duct before opening to the exterior by the excretory pore. The latter is located posterior to the genital pore.

The heart lies below the gills in the pericardial cavity. It consists of three parts: a large blood sinus, the sinus venosus into which all the blood flows from the body; a large auricle which receives the blood from the sinus venosus; and a thick walled ventricle into which the blood flows from the auricle. The ventricle pumps the blood into the gills where the exchange of gases takes place. Aerated blood from the gills returns to the body through the arteries. Hence the heart of a fish is entirely a venous heart.

DISTRIBUTION

The white crappie is one of the most abundant of the sunfish family. It is common all over the state in our large reservoirs, streams and lakes, and to a smaller extent in our small lakes and reservoirs. It has a wide distribution being found in the Great Lakes (excepting Ontario), southward through the Mississippi Valley to Alabama and Texas, and westward to Kansas and Nebraska. In recent years it has been transplanted east of the Alleghanies where formerly it was quite rare. It is an easy fish to propagate. It thrives in fairly warm water in shallow lakes and reservoirs where the bottom may be muddy. Adequate vegetation is not essential to its existence. White crappies reach a length of about 13¼ inches or more in Buckeye Lake. Specimens weighing 2½ pounds and 17 inches in length have been taken from some of the large reservoirs.

SCHOOL MOVEMENTS

Judging from the test net catches and creel census reports, the white crappies, like the bluegill, travel in schools and are quite active along the shore from early March through June and early July, and during the autumn months. They are active along the shore during the spawning period, April, May, June, and early July as shown by the test net catch and the fisherman's catch (Fig. 11). Like the bluegill, the activity of the white crappie along the shore reaches a low ebb towards the end of the spawning period, and continues so during late July and August. In Spetember they become quite active, and continue to be active along the shore well into the winter months. During July and August when the water temperature reaches 87 degrees Fahrenheit, the crappies are inactive. During this period both the test net catch and creel census are low. This may be due to a lowered oxygen supply, increase in water temperature, and lessened food needs, or other factors which are not clearly understood.

ASSOCIATIONS

As shown by the test net catch (Fig. 11), the white crappie is associated both diurnally and nocturnally with the black crappie, the white bass, bluegill, brown bull catfish, the channel catfish, and the gizzard shad.

REPRODUCTION

Attainment of Sexual Maturity

The age at which sexual maturity is attained in fishes varies. The pumpkin seed sunfishes spawn the second summer when they are one year old. Bluegills that reach a length of 3 to 3½ inches also spawn the second summer or when they are one year old. This was determined in an experiment conducted by the author at the Ohio State Kincaid Fish Hatchery at Latham during 1951–1952. It appears, as many believe, that sexual maturity is a matter of growth, that when a fish reaches a certain length it will begin to spawn irrespective of age.

Buckeye Lake's white crappies do not spawn until they are two years old or even three years old. Of 48 one year old white crappies observed in this study, we found no mature specimens. Of the 27 two year old specimens, only one had

mature eggs. The total length of this fish was 5⅝ inches. Hanson (7) states that sexual maturity of the white crappies of Illinois is attained during the second and third years, or at the age of 24 and 36 months. There is no indication that white crappies in Illinois ever spawn when one year old. However, spawning when one year old has been observed in Texas black crappies, Harper (9). Also, only about a third of the two year old white crappies from Lake Chautauqua examined by Mr. Hanson appeared to be approaching maturity. In a sample of 127 two-year-old females examined on May 16, 1940, dissections showed that the ovaries of only 40 contained well developed eggs, while the ovaries of the other 87 females were still in an immature condition. He believed none of this latter group would reach maturity until the following year, or when they were three years old. Also it is interesting to note that the 40 mature females averaged 6.2 inches total length, while the immature females, in which the eggs were undeveloped, averaged only 5.8 inches.

Eschmeyer, Stroud, and Jones (4), in a study of two year old white crappies from one of the Tennessee Rivers, found some of the fish were mature while others were immature.

SEASONAL COLORATION

The coloring of the male and female white crappies is the same except during the spawning season. During this time the male is usually much darker than the female. The dark pigmentation begins to appear in April and becomes more pronounced as the spawning season progresses. By the end of June it begins to disappear. Usually by the end of July both males and females again look alike. However, there may be exceptional cases where the pigmentation is retained longer. The deepest color appears on the sides of the head, mandible, and breast. It is less pronounced on the sides of the body.

SPAWNING PERIOD

The extent of the spawning period was determined by comparing the ratio of body weight to ovary weight.

The spawning period varies in different parts of the country. Forbes and Richardson (6) observed white crappies spawning in Havana, Illinois, in May. Hanson (7) observed white crappies nesting at Lake Springfield, Illinois, on May 26, 1941. Eddy and Surber (3) gave late spring and early summer as the spawning period in Minnesota.

According to Eschmeyer and Smith (4) the white crappie spawning period may be prevented or delayed by subjecting the fish to continued low water temperatures.

According to Hanson (8) white crappies spawn in Illinois in May and June, the height of the spawning period being late May and early June. He found ripe males as early as May 16 and as late as June 24, while ripe females were found as early as May 6 and as late as July 13. In my work, 462 males and females of all sizes were dissected and examined during 1950, 1951, and 1952, from March to November.

A fairly accurate method of determining the extent of the spawning period is
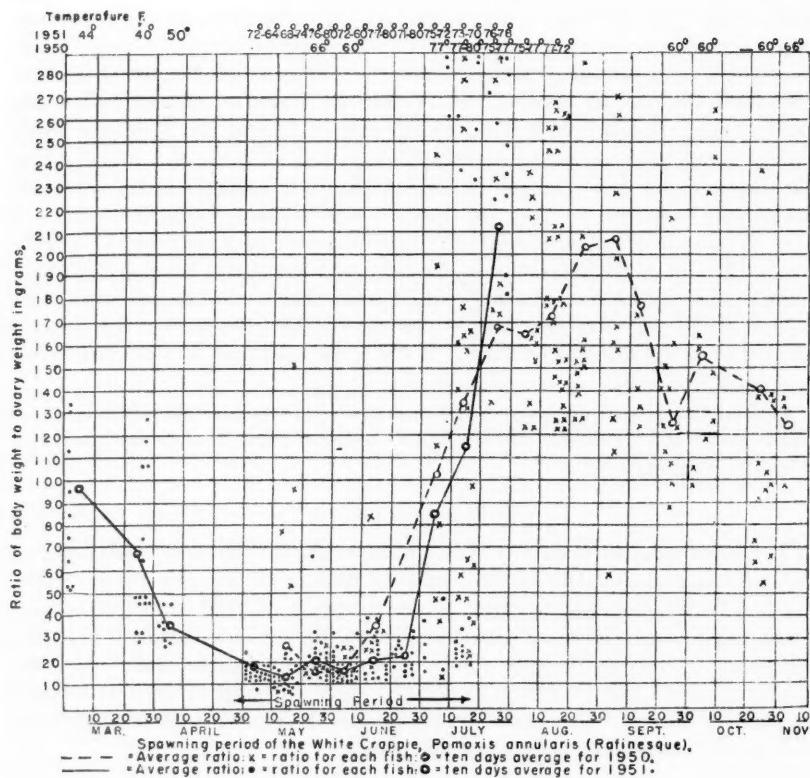
FIG. 2

by comparing the ratio of body weight to ovary weight. The white crappie begins to spawn in Buckeye Lake during April. The body weight–ovary weight ratios of fishes taken on March 1 ranged from 50 to 132 with an average ratio of 98 (Fig. 2). On March 28 the ratios dropped as low as 28 and a range of 28 to 126. In April the ratios ranged between 26 and 45. Fishes with a ratio of 28 were almost ripe and ready to spawn. On May 2 the average body weight–ovary weight ratio was between 12 and 22. The majority of the crappies were ripe males and females. The average ratio between May 2 and May 10 was 17, which indicates accelerated spawning activities. The spawning period continued actively through May and June and gradually diminished through the early part of July. Mature females were taken as late as July 20. Then the ratio of body weight–ovary weight began to increase. By the middle of August the ratio was 260. In September it began to drop and continued to drop through November. The average ratio in November was 125 as compared with 98 the following March. By March 25 the average body weight–ovary weight ratio had dropped to 68 indicating a growth

of the eggs in preparation for spawning. The temperature range of the water during the spawning period varied from 51°F. in early April to 80° in late June.

NESTING HABITS

Very little is known of the spawning behavior and the nest building habits of the white crappie. Their tendency to spawn under overhanging banks, cliffs, and tree roots, and also their frequent use of deep water for spawning purposes make it difficult to observe their behavior during this period. The nesting site may be quite variable as to depth of the water and the kind of sub strata. Nests have been observed in water in depths ranging from 2 inches to 20 feet, and on sub strata of mud, clay, sand, gravel, and vegetation.

In Buckeye Lake, where the water is quite turbid, it is impossible to observe the spawning and nesting habits.

Hanson (7) reported white crappies spawning in Lake Springfield, Illinois on on May 26, 1941, in water 4 to 8 inches deep along an undercut sod bank of red clay. The nests were 2 to 4 feet apart and concealed from the observer along the shore by an overhanging tree. The eggs were attached to blades of lawn grass and grass roots dangling in the water only 2 inches below the surface. The fish guarding this nest was actually below the eggs. In another nest guarded by another fish about 3000 eggs were attached to a 3 inch ball of elm roots.

Nelson (11) observed white crappies nesting in 10 to 20 feet of water on rocks and boulders, submerged brush and trees at Elephant Butte Lake, New Mexico. Also, he observed white crappies spawning in water $2\frac{1}{2}$ feet to 5 feet deep in federal hatchery ponds, at Elephant Butte. The nests were quite shallow and scooped out of aquatic vegetation to which the eggs were attached. In some ponds the crappies spawned where there was no means for egg attachment.

EGG PRODUCTION

Mature eggs of the white crappies vary in size from 0.82 mm. to 0.9 mm. in diameter (Fig. 3A). Hanson (8) gave 0.89 mm. as the average diameter of the egg in his work on the white crappies of Illinois. The perivitelline space is 0.05 mm. in diameter. The yolk is granular and contains a large oil globule near the center and a cap of protoplasm at one end of the yolk.

The number of eggs in a mature fish varies with the age and size of the fish. No mature eggs were found in fish below $5\frac{7}{8}$ inches in length. Of the $5\frac{7}{8}$ size group, only one fish had mature eggs. This fish had two annular rings on the scales and was probably in its third summer's growth. Table 1 shows the egg production of the white crappies by total length and by weight groups of fishes $5\frac{7}{8}$ inches in length and weighing 13.3 grams to fishes 13 inches in length and weighing 581.1 grams. The total number of eggs produced varies from 1908 eggs in a fish $5\frac{7}{8}$ inches in length to 325677 eggs in a fish 13 inches in length. The plumpness of the ovaries varies during the spawning period. Early in the spawning period the ovaries are plump and as the season progresses the plumpness varies considerably. In some of the less plump females there were many ripe ova that could be voided easily by applying a little pressure to the sides of

STAGES IN DEVELOPMENT FROM FERTILIZATION TO 7 HOURS AFTER HATCHING

FERTILIZED EGG   2 CELL STAGE   4 CELL STAGE   5 TO 8 CELL STAGE
         BLASTODISC   YOLK   OIL
                                 MASS   GLOBULE

FIG.3A.5 MINS.   FIG.3B 50 MINS.   FIG.3C 55 MINS.   FIG.3D 1 HOUR

BLASTODERM   LATER BLASTODERM   GERM RING.YOLK PLUG   LATERAL VIEW

FIG.3E 1¼ HOURS   FIG.3F 2¼ HOURS   FIG. 3G 3¼ HOURS   FIG. 3H 5HRS.15MINS.

DORSAL VIEW   LATERAL VIEW   20 to 22 SOMITES   23 to 25 SOMITES

FIG. 3I   FIG.3J 9 HOURS   FIG.3K   FIG3L

FIG.3M 23 HOURS   FIG. 3N JUST HATCHED 27½ HOURS   FIG. 3 O 1.75 mm. 7 HOURS

FIG. 3, A–N
FIG. 3,O 1.75 mm. 7 hours after hatching.

the abdomen. The white crappie does not void all its eggs at one spawning act but may ovulate over a period of time. Many fish were taken with partially spent ovaries containing both mature and immature eggs. Whether the immature eggs continued to develop and were voided later or did mature and were reabsorbed was not determined. Ovaries that were completely spent still retained many immature eggs.

During the fall there was a considerable decrease in the body weight–ovary weight ratios. The ovaries were quite plump and contained many eggs in early stages of development. The body weight–ovary weight ratios in the fall and early spring were about the same.

TABLE 1

Egg Production in the White Crappie

AVERAGE LENGTH	AVERAGE WEIGHT	NUMBER OF FISH	AVERAGE OVARY WEIGHT	RATIO OF BODY WEIGHT TO OVARY WGT.	AVERAGE NUMBER OF MATURE EGGS	AVERAGE NUMBER OF IMMATURE EGGS	AVERAGE TOTAL NUMBER OF EGGS PER FISH
inches	grams						
5⅞	43.3	1	3.5	12.4	970	938	1908
6¼	51.5	3	3.0	17.2	8118 (3*)	13012 (2*)	13591
6½	58.8	5	5.3	11.1	12245 (3*)	5819 (3*)	23683
6¾	60.8	10	4.4	13.8	14350 (9*)	11246 (10*)	24172
7	68.0	10	5.0	13.6	16320	10499	26819
7¼	72.6	6	5.8	12.5	24484	10171	34656
7½	75.1	3	5.3	14.2	18577	6876	25527
7¾	90.0	1	5.1	17.6	20655	2160	22815
8¼	119.8	2	10.4	11.5	32042	20272	52314
8½	125.9	2	10.7	11.8	32200	11444	43644
8¾	135.5	2	16.5	8.2	63365	11065	74460
9¼	182.2	1	14.2	12.8	52471	16988	69459
9⅜	154.8	1	17.1	9.0	60474	948	61418
9¾	247.0	2	23.0	10.1	106365	26972	133634
10	199.9	2	13.6	14.7	40119	16992	57111
10¼	256.6	2	20.3	12.6	122645 (1*)	102675 (1*)	152205
10½	245.2	2	16.4	15.0	60820	33829	94649
10⅞	325.0	1	32.0	10.1	95046	2041	97090
11½	320.8	2	29.3	10.9	159145	126447	206020
11¾	462.2	1	53.3	8.6	125000	118916	243916
13	581.1	1	49.0	11.9	213213	112464	325677

* Indicates the number of fishes used for the count. In some cases it was impossible to separate mature from immature eggs. In some fishes only immature eggs were present.

VIABILITY OF THE SPERMS

The viability of the sperms was determined by placing a drop of water containing sperms on a glass slide and observing the duration of the active period through the microscope. The length of time during which they remained active varied from 2 minutes to 2 minutes and 45 seconds. However, this does not mean that a sperm is capable of penetrating the egg membrane and fertilizing the egg during this entire period.

EMBRYONIC DEVELOPMENT

Eggs and sperms were removed from gravid females and mixed in culture dishes filled with water. The temperature of the water was kept at 70° to 72° Fahrenheit during the entire incubation period. As soon as the eggs were fertilized

they were distributed into several dishes to avoid crowding. The water was changed every few hours. Unfertilized eggs were removed with a medicine dropper to prevent contamination. Culture dishes are convenient for watching early stages of development under the binocular microscope. Also a greater percentage of hatching was obtained by this method than through the use of larger dishes or aquaria.

Observations were made of the developmental stages from the fertilized egg through 14 days after hatching. Drawings were made from direct observations of the living specimens. Also some post larvae were stained with paracarmine. These stained specimens were excellent for a study of the development of internal organs.

PERIOD OF INCUBATION

As in the bluegill sunfish the early development of the white crappie is quite variable. Although fertilization must have taken place within three minutes, the first two cell state does not appear until 50 minutes later. Three and a half hours later all stages of development are present from the two cell stage to early blastula.

The hatching time of the white crappie kept at a temperature of 70° to 72° Fahrenheit varies from 24 to 27½ hours. This is much shorter than the hatching time of the bluegill which varies from 31 hours and 50 minutes to 62 hours at a temperature of 72° to 74°F. The white crappie is not as well developed as the bluegill at hatching. At this time the bluegill embryo more than encircles the yolk sac. Both the head and tail are free and are capable of vigorous movements, which are chiefly responsible for the rupturing of the egg membrane. The young larvae pop out of their shells like corn popping and begin swimming furiously in circles. The discarded egg membranes are quite thick and do not stick to the larvae. Hatching continues over a period of 31 hours. The white crappie embryos hardly encircle the yolk at hatching and their movements are quite feeble. The head is still attached to the yolk. The tail is free and is capable of some movement. At hatching they were so poorly developed that I did not expect them to live. However, they continued to develop normally. They do not pop out of the egg membrane as do the bluegills. The membrane, unlike that of the bluegill, is like an elastic bag which changes its shape with every movement of the embryo, and finally dissolves into a sticky mass to which the young larvae remain attached head on for some time after hatching. The egg membranes stick together into one large mass. As many as fifty young larvae were attached at one time to this sticky mass. This dissolving of the egg membrane in the white crappie may be due to the presence of an enzyme within the perivitelline space as was suggested by Dr. John Price, Ohio State University, in his discussion of the egg membrane of the white-fish Coregonus clupeaformis.

CLEAVAGE STAGES

Twenty minutes after fertilization the protoplasmic disc becomes constricted into a well defined caplike blastodisc (Fig. 3A). By 50 minutes the first cleavage furrow appears dividing the blastodisc vertically into two blastomeres of about

equal size (Fig. 3B). Five minutes later a second furrow appears at right angles to the first to form the 4 cell stage (Fig. 3C). Following this the cleavage furrows appear rapidly so that by 3¼ hours the cells have enveloped almost half of the yolk (Fig. 3D, E, F, G). By five hours and 15 minutes the blastoderm has grown over the equator of the yolk and the embryo is beginning to take form (Fig. 3H, I).

DIFFERENTIATION OF THE EMBRYO

Nine hours after fertilization. Ten to twelve somites are now present. The brain can now be recognized and optic evaginations are present laterally. No optic vesicles are yet visible (Fig. 3J).

Sixteen hours and fifteen minutes. There are now 20 to 22 somites present. The brain is three parted. The eyes are better developed and the optic capsules are beginning to appear. Nasal capsules are also present (Fig. 3K).

Twenty one hours and fifteen minutes. The embryo has not yet completely covered the yolk. There are 23 to 25 somites present (Fig. 3L).

Twenty three hours. The embryo has almost completely covered the yolk. The circulatory system is not yet clearly defined. The tail is now moveable. The heart action is quite pronounced (Fig. 3M).

Twenty seven and a half hours. Just hatched. The egg membrane is quite elastic. The movement of the tail is more pronounced. The heart action is rapid. From the external view the circulatory system is still indistinct except in the region of the heart and beneath the gills. In some forms the egg membranes are beginning to rupture at the head end and the young larvae are slowly squeezing their way out. They remain partly coiled about the yolk and are still attached to the egg membrane at the head end (Fig. 3N). The movements are feeble compared with the vigorous movements of the newly hatched bluegill larvae. Three hours later the larvae are still partly coiled about the yolk. The length at hatching varies from 1.215 millimeters to 1.98 millimeters.

LARVAL AND POST LARVAL DEVELOPMENT

1.75 millimeter stage (Fig. 3O). The larvae are now straightened out and are capable of much movement. The discarded egg membranes are still a sticky mass, and the larvae become attached head on whenever they come in contact with it. As many as fifty larvae may be attached at one time. The heart action is much stronger and the circulation of the blood can now be followed all over the body.

3 millimeter stage (Fig. 4A). Thirty nine hours post hatching. The brain is five parted. The digestive tube can be followed from the vent to the mouth region. The jaws are not yet evident externally. Gill clefts are appearing in the pharynx. The optic and otic capsules are well developed. The fin fold extends from the head over the tail to the vent. There are no fin rays in the caudal fin. The heart is quite active. The auricle and ventricle and ventral aorta are well defined. There is no evidence of an air bladder from the external view. Pectoral fins are not present. Semicircular canals are present in the otic capsules.

3.7 millimeter stage (Fig. 4B). Two days nine hours after hatching. Pectoral

LARVAL AND POST LARVAL DEVELOPMENT, WHITE CRAPPIE
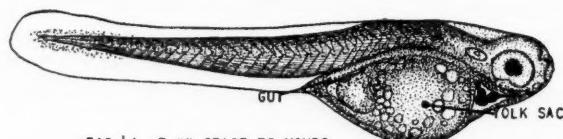
FIG. 4A. 3 MM. STAGE 39 HOURS
POST HATCHING
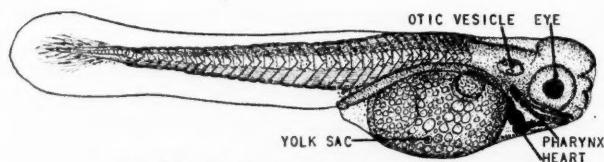
FIG. 4B. 3.7 MM. 2 DAYS 9 HOURS
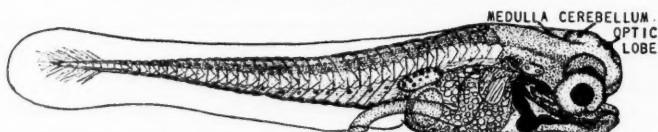
FIG. 4C. 3.9 MM. STAGE, 4 DAYS 10 HOURS
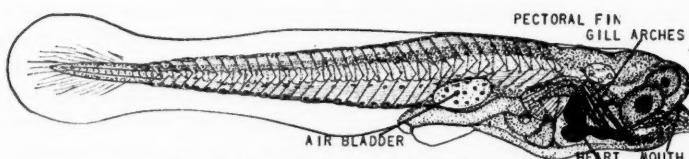
FIG. 4D. 4 MM. STAGE, 8 DAYS 9 HOURS
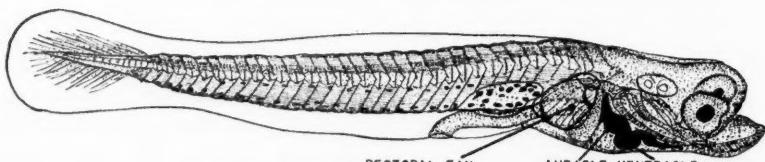
FIG. 4E. 4.2 MM. STAGE, 10 DAYS
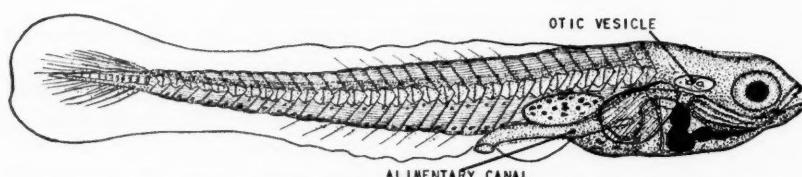
FIG. 4F. 6 MM. STAGE, 14½ DAYS

FIG. 4

fins are now well defined above the anterior end of the yolk sac. The brain plexuses are evident. The pharynx and mouth are better developed. The jaws are present but are not moveable. Fin rays are appearing in the caudal fin.

3.9 millimeter stage (Fig. 4C). Four days ten hours after hatching. The jaws are now well developed and are moveable. The gill arches and gill filaments are present. The pectoral fins are well developed. The air bladder is now visible above the posterior end of the yolk sac. The alimentary canal is beginning to fold in the region of the yolk sac. Pigment spots are appearing along the hypaxial muscles as well as within the air bladder. The young larvae are now quite active.

4 millimeter stage (Fig. 4D). Eight days and nine hours post hatching. At this stage there is only a slight increase in length. The air bladder is longer and there is a greater folding of the alimentary canal.

4.2 millimeter stage (Fig. 4E). Ten days post hatching. The jaws are now well developed and quite moveable. The circulatory system is very well defined. The body movements are quite vigorous. Fin rays are beginning to appear in the dorsal and ventral fin folds.

6 millimeter stage (Fig. 4F). Fourteen days and twelve hours post hatching. There are now indentations in the free margins of both the dorsal and ventral fin folds indicating the beginning of the differentiation of the dorsal and anal fins. The pectoral fins are now well developed. There is no evidence of the pelvic fins from the external view. The caudal fin is beginning to take the shape of the adult homocercal tail. The jaws and gill arches are now well developed.

AGE AND GROWTH

Considerable work has been done on the age and growth of the white crappie in Ohio waters. E. L. Wickliff (13), and Roach and Evans (12), give the length and weight relationships of most of our game fishes in both liberalized fishing lakes and in non liberalized fishing lakes of Ohio. In this paper 664 white crappies ranging in length from 2 inches to $13\frac{1}{4}$ inches were studied. All of these fishes, with the exception of those with only one annulus, were caught in a six foot fyke net. Fishes having only one annulus were taken by seining. All were taken to the laboratory where they were weighed, measured, sex determined and the number of annuli determined for each fish. The group included fishes with one to seven annuli.

Formation of the Annulus

Age determination by counting the number of annuli present is difficult in the white crappie, since the annulus may be formed over a period of several months, or not at all during some years. Also, false annuli may be present. According to Hanson (8), from evidence obtained at Lake Decatur, Illinois, the white crappie does not always form an annulus each year. Some crappies that fail to grow during a particular year do not form an annulus at this time. On the other hand, some fish may form two annuli in one year, one of which is false and probably due to starvation. In this study, in order to determine the time when the last annulus was formed, the growth after the last annulus was determined at the time when

TABLE 2
Annulus Formation

MONTH	NUMBER OF FISHES	GROWTH AFTER ANNULUS FORMATION	
		.3 inches or less	Annulus on margin
March......................	16	3	
April.......................			
May.......................	90	16	1
June.......................	40	8	1
July.......................	44	8	1
August.....................	12	5	3
September..................	62*	4	1
October....................	13	5	
November..................	4	1	

* Includes 40 fishes of only one annulus.

the fishes were caught. Those that grew 0.3 of an inch or less after the formation of the last annulus during a particular month were assumed to have formed the annulus that month or late the preceding month. However, it is realized that this procedure is not too accurate, because fishes, even of the same brood, do not grow at the same rate. From the results of this study (Table 2) it appears that the annulus may form from early March through the summer to early fall. Most of these fishes formed their annuli during the late summer or early fall. Fishes that had made no growth after the formation of the last annulus were found from May to September inclusive. The September results, which include 40 fishes with only one annulus, seem to indicate that as a rule younger fish form their annuli early in the summer. If the fishes with one annulus are disregarded, 22 of the fishes would have been taken, and 4 would have grown less than 0.3 of an inch.

Growth at Each Annulus

For the study of the growth at each annulus scales were examined from 276 fishes from above the lateral line from a point below the anterior margin of the dorsal fin. The scales were placed between two microscope slides held together with scotch tape. They were projected on a screen by means of a rayoscope and the number of annuli determined and recorded. The growth at each annulus was determined by measuring the distance from the scale focus to each annulus, and from the focus to the margin of the scale. The length of the fish at each annulus was then calculated by the formula given on page 115.

The average growth of both male and female white crappie is about the same for the first five years (Fig. 5).

During the sixth year and seventh year the females grew faster than the males. However, this difference may be due to the fewer numbers of male specimens that were included in the six and seven year groups.

The annual increment for the first year is greater than in any successive year (Table 3).

Yearly Growth of Male and Female
White Crappies

Age—Number of years
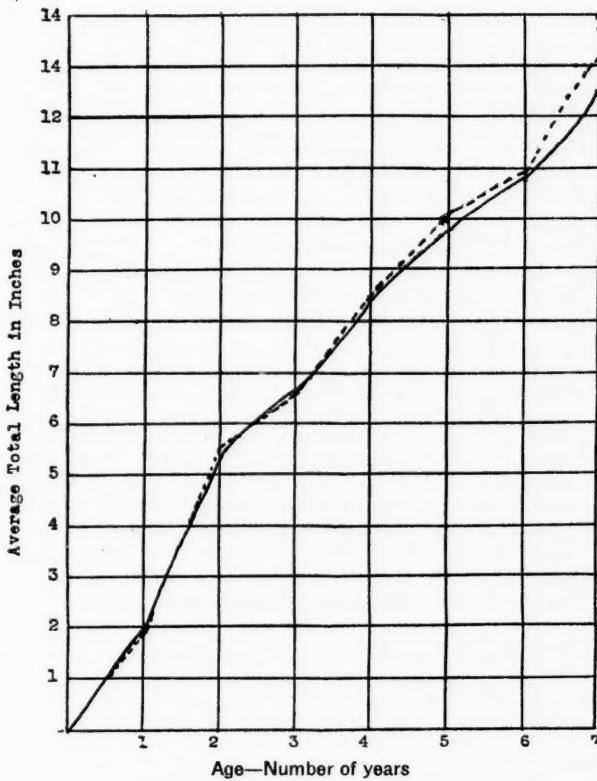
Fig. 5 The curves are graphs of the yearly growth
Male———
Female----

Following the first year's growth there is a gradual decrease in the yearly increment during each ensuing year with the exception of the fourth year and the seventh year.

LENGTH AND WEIGHT RELATIONSHIPS

Table 4 and Figure 6 give the average length and weight relationships in ¼ inches. These relationships are given for both sexes, also the average of both sexes combined. A total of 664 specimens were examined of which 295 were males and 369 were females. The sex of the fish was determined by dissection in the laboratory. For convenience, the weight is given both in grams and in ounces. For the purpose of comparison the length and weight of the white crappies taken in 1934 are also given at the bottom of the table, Wickliff (13).

TABLE 3

Average Length at Each Annulus, Length Range and Annual Increment

YEAR GROUP	Sex	Number	1	2	3	4	5	6	7	Range	Average
			AVERAGE LENGTH IN INCHES AT EACH ANNULUS							TOTAL LENGTH	
I	Male	30	2.13							2.37–3.37	2.97
	Female	18	2.19							2.37–3.37	2.95
II	Male	16	2.41	4.67						4.75–5.75	5.33
	Female	11	2.31	4.50						5.00–5.87	5.49
III	Male	32	2.30	4.29	6.03					5.25–7.62	6.63
	Female	35	2.08	4.06	5.80					5.25–8.37	6.61
IV	Male	31	2.28	4.27	5.98	7.95				7.17–10.00	8.41
	Female	38	2.34	4.21	6.46	7.87				7.00–10.25	8.45
V	Male	20	2.32	4.24	6.02	7.69	9.17			9.00–11.00	9.77
	Female	27	2.31	4.17	6.02	7.71	9.15			7.87–13.25	10.10
VI	Male	10	1.95	3.60	5.37	7.19	8.90	9.40		10.25–11.25	10.75
	Female	15	2.25	3.86	5.47	7.05	8.88	10.13		10.37–11.75	10.94
VII	Male	1	1.99	4.20	5.53	7.75	8.85	9.95	11.28	11.50–11.50	11.50
	Female	2	2.21	4.16	5.92	7.91	9.86	11.28	12.47	13.00–13.25	13.12
Average	Male	140*	2.25	4.21	5.78	7.64	8.97	9.67	11.28		
	Female	136*	2.25	4.16	5.93	7.63	9.29	10.70	12.47		
Average	Male & Female	276*	2.25	4.18	5.85	7.63	9.13	10.18	11.87		
Annual	increment		2.25	1.93	1.67	1.78	1.50	1.05	1.69		

* Total number.

It is interesting to note that the length and weight relationships for 1934 and 1951 are about the same. The average weight of a 7 inch male for 1951 was 2.3 ounces. The average weight of a 7 inch female was 2.4 ounces. The average length and weight relationship for a 7 inch white crappie for 1934 was 2.42 ounces.

PLUMPNESS OR K VALUES

The condition of plumpness, or K value, was determined from an examination of 592 fishes ranging in length from 2 to 11 inches. These are placed in classes. For example, fishes 3.6 inches to 4.5 inches in length are placed under class center 4 inches. Those ranging in length from 5.6 inches to 6.5 inches are placed under class center 6 inches. The same plan is followed for all lengths above and below these figures.

During 1950, only 2 fishes below 4 inches in length are included. During 1951,

TABLE 4
Length and Weight Relationships, 1951

TOTAL LENGTH IN INCHES	NUMBER		AVERAGE WEIGHT					
	Male	Female	Male		Female		Both Sexes	
			Grams	Ounces	Grams	Ounces	Grams	Ounces
2.0	1		1.6	0.05			1.6	0.05
2.25	1	1	2.1	0.07	2.2	0.07	2.2	0.07
2.50	7	6	2.8	0.1	2.9	0.1	2.8	0.1
2.75	11	9	3.6	0.12	3.4	0.12	3.5	0.12
3.0	11	6	4.6	0.17	4.8	0.17	4.5	0.17
3.25	6	4	5.6	0.2	5.6	0.2	5.6	0.2
3.50		1			7.2	0.25	7.2	0.25
3.75								
4.0								
4.25	.	1			14.1	0.5	14.1	0.5
4.50								
4.75	3		22.4	0.8				
5.0	3	4	26.7	0.95	25.9	0.9	26.3	0.9
5.25	2	5	30.9	1.1	28.0	1.0	29.0	1.05
5.50	10	7	33.7	1.2	31.6	1.1	32.8	1.15
5.75	10	7	37.8	1.3	36.0	1.4	37.0	1.35
6.0	14	22	43.9	1.5	44.7	1.6	43.4	1.55
6.25	15	24	47.7	1.7	49.4	1.7	48.8	1.70
6.50	21	33	53.3	1.9	53.6	1.9	53.5	1.9
6.75	25	39	59.5	2.1	59.6	2.1	59.5	2.1
7.0	17	39	67.3	2.3	67.6	2.4	67.5	2.35
7.25	13	25	71.6	2.5	73.4	2.6	72.9	2.55
7.50	13	16	85.4	3.0	80.9	2.8	82.9	2.9
7.75	16	15	95.1	3.3	100.7	3.6	97.7	3.45
8.0	12	10	109.1	3.8	104.1	3.8	106.8	3.8
8.25	13	9	118.6	4.2	113.5	4.0	116.5	4.1
8.50	11	9	129.9	4.5	124.5	4.4	127.4	4.45
8.75	11	10	137.3	4.8	138.5	4.9	137.9	4.85
9.0	12	7	147.3	5.1	154.5	5.5	149.9	5.3
9.25	4	7	174.2	6.1	163.7	5.8	167.6	5.95
9.50	3	6	185.3	6.5	177.8	6.3	180.2	6.4
9.75	7	4	182.8	6.4	194.0	6.9	187.4	6.65
10.0	4	7	222.5	7.8	202.7	7.2	209.8	7.5
10.25	5	8	250.0	8.8	229.4	8.0	237.0	8.4
10.50	5	7	249.2	8.8	240.0	8.5	244.1	8.65
10.75	4	5	275.5	9.7	254.1	9.0	263.6	9.3
11.0	3	5	343.3	12.1	285.9	10.0	307.9	11.05
11.25		4			318.0	11.2	318.0	11.2
11.50	2	3	341	12.0	326.3	11.5	332.3	11.75
11.75		2			425.0	15.0	425.0	15.0
13.0		1			581.1	20.0	581.1	20.0
13.25		1			521.2	18.3	521.2	18.3
	295	369						

Length and Weight Relationship, 1934, E. L. Wickliff (13)

Total length in inches 5.80 6.20 6.60 7.0 7.4 9.0 9.8 10.2 11.0
Weight in ounces 1.40 1.60 2.00 2.42 2.93 6.24 7.07 8.57 10.6

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Length-Weight Relationship
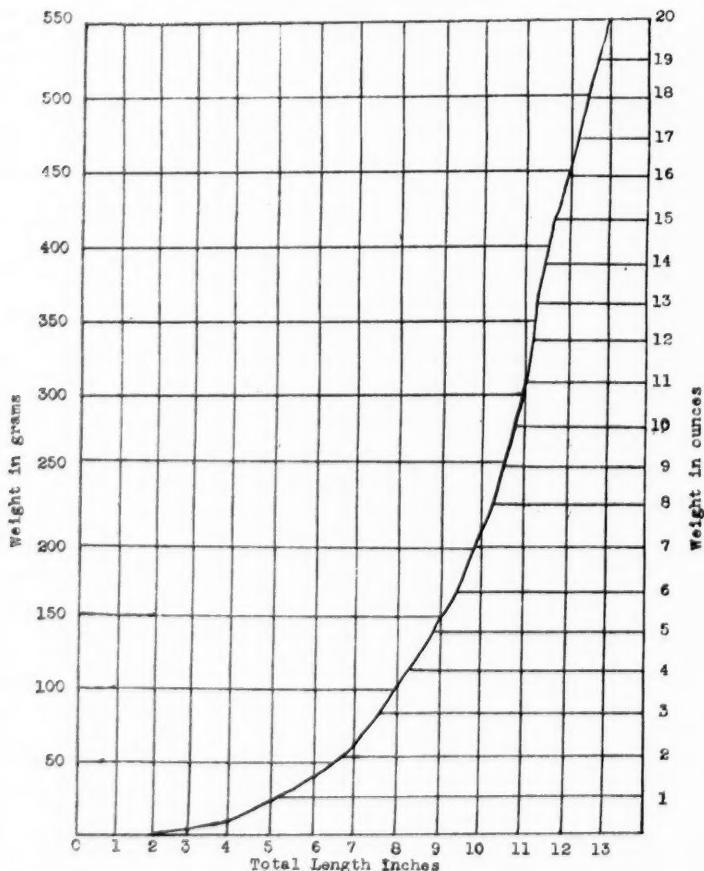
FIG. 6 Length-weight relationship of the white crappie. The curve is the graph of the length-weight equation.

54 fishes with a class center of 2 inches were examined. The high and low K values, 2.18 and 1.9, appeared in July and August respectively, (Table 5 and Fig. 8). This low K value for late summer was also observed in white crappies of Lake Decatur, Illinois, Hanson (8).

During 1950, the K values of the 4 inch class center increased from 2.29 in June to 2.38 in July. During August there was a drop to 2.15. This loss occurred during the period of inactivity when both the creel census and the test net catch were low (Fig. 11). Following this period, the K value increases and reaches a

high of 2.99 in November. During 1951 only 2 fishes of the 4 inch class center were taken (table 5 and Fig. 8).

In the 1950 5 inch group the condition of plumpness follows the same pattern as in the 4 inch class with a high K value in June and July followed by a low value in August. During September, October, and November, the K values again reach a high peak. In the 1951 5 inch group, the high is reached a month earlier in May. This is also time of the low K value which occurs in June and July instead of August.

Fishes taken in 1950 of the 6 inch and 7 inch classes follow the same general trend. After reaching a summer high plumpness in July, the K value drops in August, then reaches a high in November. The 1951 6 inch and 7 inch classes follow the same trend as the 1951 five inch group, the high and low K values occurring a month earlier. This may be due to the early spring weather of 1951.

In the 1950 8 and 9 inch groups there are high K values in May. The low K value in the 8 inch group occurs in August followed by a high in September, October, and November. The summer low in the 9 inch class occurs in July rather than in August. Another low occurs in September.

From these observations it appears that the general trend in high and low K values follows the same pattern in most groups with a few exceptions. During spring and early summer, the K values are high. There is a drop in August followed by another high in September, October, and November.

Also, it appears that the larger fishes have higher K values. This relationship was also observed by Hanson (8) in the white crappies of Lake Decatur, Illinois. This trend is also true of the small mouth bass, and the large mouth bass.

Table 5 and Figure 9 show the comparative K values in male and female white crappies. The males appear to be plumper than the females except for a short period in May. This tendency toward higher K values in males was also observed by Hanson (8).

Table 6 is a comparison between the K values of white crappies of Lake Decatur, Illinois, and white crappies of Buckeye Lake, Ohio. The K values of Lake Decatur are higher in all classes with the exception of the 10 inch class and the 11 inch class. However the few specimens included in these two classes make these data inconclusive.

POSSIBLE CAUSES FOR K INCREASE AND K LOSS

There appears to be a relation between the K increase and K loss and the spawning activities of the white crappie. Figure 10 shows the relation between the K values and the ratio of body weight to ovary weight. Note that when the body weight and ovary weight ratios are low during the spawning period, the K values are high. As the spawning period progresses in May and June, and the ovaries become spent, the body weight ovary weight ratios are high and the K values of the fish are low.

Also the abundance of food and the feeding activities are important factors in K loss and K increase. During the early spring when the crappies are actively

TABLE 5

Seasonal Fluctuations in the Coefficient of Condition (K) in Buckeye Lake White Crappies of Different Length Classes. Figures in Parentheses Represent Numbers of Specimens

Standard length in inches. Class center: for example, the 7-inch class includes fish of 6.6 to 7.5 inches

1950	Sex	2	3	4	5	6	7	8	9	10	11	K Average
May 13–31 Average	F		2.21(1)		2.25(3)	2.23(1)	2.09(1)	3.39(3)	2.91(2)	3.15(1)	2.68(1)	2.66(11)
	M		2.21(1)		2.01(3)	2.20(6)	2.09	3.10(2)	3.11(2)	3.15	2.68	2.53(15)
	A		2.21(1)		2.23	2.21		3.09	3.01			2.59(26)
June 4–17	F			2.29(2)	2.30(2)	2.33(1)	2.42(4)	2.55(6)	2.84(1)			2.49(14)
	M			2.29(2)	2.37(4)	2.48(3)	2.36(3)	2.56(3)	2.66(2)			2.45(17)
	A				2.33(6)	2.40	2.39	2.55	2.75			2.47(31)
July 7–26	F			2.37(6)	2.39(7)	2.53(11)	2.48(6)	2.39(2)	2.29(2)			2.41(34)
	M			2.40(10)	2.35(7)	2.49(12)	2.46(12)	2.41(6)	2.75(2)			2.48(49)
	A			2.38	2.37	2.51	2.47	2.40	2.51			2.44(83)
Aug. 8–25	F			2.15(3)	2.23(18)	2.32(6)	2.32(3)	2.41(2)	2.70(2)			2.28(32)
	M				2.24(15)	2.40(6)	2.35(6)	2.32(3)	2.70			2.40(32)
	A			2.15(3)	2.23	2.36	2.33	2.37				2.34(64)
Sept. 6–29	F			2.40(2)	2.45(12)	2.54(10)	2.45(5)	2.50(1)	2.24(1)			2.41(30)
	M			2.53(2)	2.46(12)	2.49(4)	2.92(4)	2.50	2.70(1)			2.60(24)
	A			2.46	2.45	2.51	2.68		2.47			2.50(54)
Oct. 3–31	F			2.99(1)	2.42(10)	2.55(6)	2.90(2)	2.48(3)				2.59(21)
	M			2.99(1)	2.41(13)	2.45(7)	2.83(6)	2.66(2)				2.67(29)
	A				2.41	2.50	2.86	2.55				2.66(50)
Nov. 2	F				2.60(2)	2.53(1)		2.88(3)	2.30(1)			2.45(3)
	M				2.60	2.53		2.88	2.30			2.70(2)
	A											2.57(5)

TABLE 5—Continued

1951	Sex									
March 1–28	F	2.32(18)	2.63(2)	2.54(4)	2.09(1)	2.16(4)	2.19(7)			
	M	2.38(20)	2.17(1)	2.86(1)	2.45(8)	2.38(3)	2.05(7)			
	A	2.35(37)	2.40	2.70	2.27	2.27	2.12			
April 6–20	F	2.72(5)	3.08(1)	2.52(4)	2.37(4)	2.62(2)	2.11(1)			
	M	2.46(10)			2.58(3)					
	A	2.56(15)	3.08(1)	2.52	2.47	2.62	2.11			
May 2–31	F	2.49(67)	2.69(9)	2.38(1)	2.41(18)	2.40(15)	2.59(14)			
	M	2.41(26)		2.27(4)	2.34(7)	2.43(9)	2.58(6)			
	A	2.47(93)	2.69	2.32	2.37	2.41	2.58			
June 1–28	F	2.19(67)	2.63(1)	2.30(2)	1.91(1)	2.26(31)	2.32(24)	2.20		
	M	2.39(21)			2.28(3)	2.27(10)	2.38(7)			
	A	2.32(79)	2.63	2.30	2.09	2.26	2.35			
July 2–28	F	2.29(42)		2.26(1)	2.42(3)	2.35(19)	2.23(18)	2.35		
	M	2.31(30)				2.40(10)	2.29(16)			
	A	2.29(72)			2.42	2.37	2.26			
Aug. 9–11	F	1.93(8)							2.18(3)	1.93(8)
	M	1.89(10)								1.89(10)
	A	1.91(18)							2.18	1.91
Sept. 1	F	2.00(18)							2.00(11)	1.99(7)
	M	1.96(30)							1.99(21)	1.94(9)
	A	1.97(48)							1.99	1.96

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Number of fish included in the survey
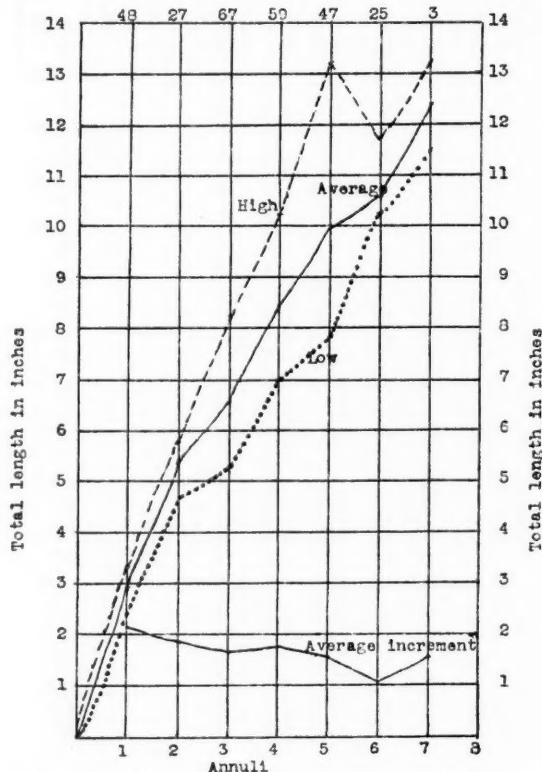
FIG. 7 The curves are the average length, **length** range and yearly increment at each annulus for the white crappie. 1951.

feeding after the winter of inactivity, the K values increase. During late July and August when the creel census and test net catch are low indicating decreased movements and feeding activities, the K values drop (Fig. 10). Beginning in September when the fish are again active, the K values increase and reach a peak in November.

Another possible cause for K loss in late summer may be due to an increase in growth in length during late July and August without a corresponding increase in breadth, Hanson (8).

FOOD HABITS

Information concerning the food habits of the white crappies was obtained through an examination of the stomach contents of 273 fishes. They were taken from test nets and by seining from March through August of 1951. They varied
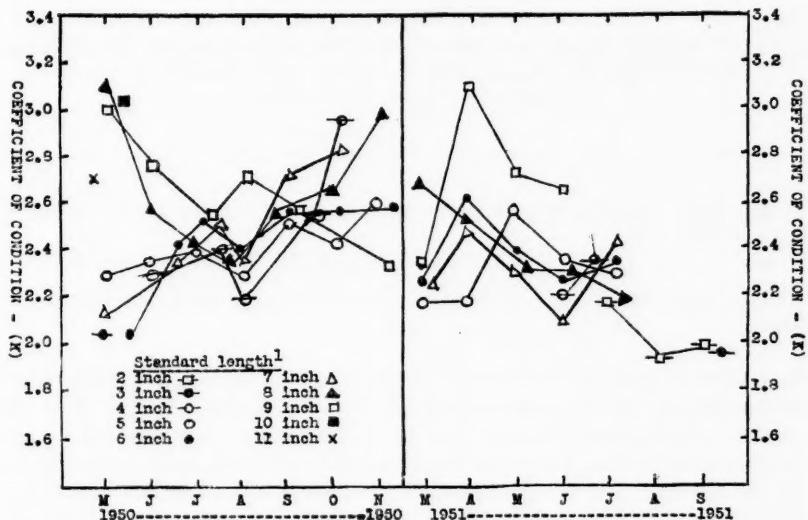
FIG. 8 Monthly fluctuations in the coefficient of condition (K) for white crappies of different length classes at Buckeye Lake.

1 Class center: for example, the 7-inch class includes fish 6.6 through 7.5 inches in length.
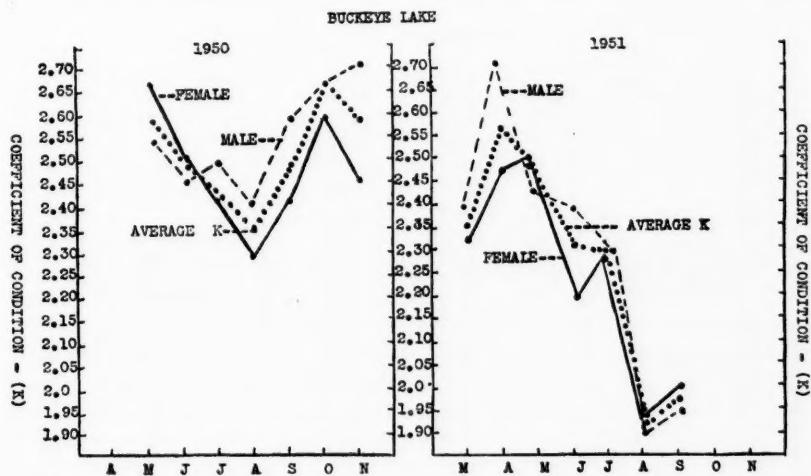
FIG. 9 Monthly fluctuations in the coefficient of condition (K) of the male and female white crappie.

TABLE 6

Average K Values of Buckeye Lake White Crappies, May to November, 1950, Compared with Those of Lake Decatur, Illinois, April to December, 1936. Figures in Parentheses Represent Numbers of Specimens

LAKE	STANDARD LENGTH IN INCHES*						
	5	6	7	8	9	10	11
Buckeye Lake, Ohio.	2.40 (208)	2.41 (177)	2.40 (100)	2.54 (53)	2.65 (31)	3.15 (1)	2.68 (1)
Lake Decatur, Illinois.............	2.60 (139)	2.88 (284)	3.00 (382)	3.00 (298)	3.09 (5)	3.09 (5)	2.57 (1)

* Class center: for example, the 6 inches class includes fish of 5.6 through 6.5 inches in length.

in size from 6 inches to 12 inches total length with the exception of those taken during August. The latter varied in length from 2 to 3 inches. Most of the stomachs examined contained food. In a few cases the food was digested beyond positive identification. However, though partially digested, the identification of the gizzard shad, Dorosoma cepedianum, was easily determined by the presence of the gizzard-like stomach and by the numerous diverticula of the alimentary canal. Table 7 shows the average estimated percentage of the food organisms ingested. It is interesting to note that the white crappies feed primarily on young gizzard shad, small crustaceans, and chironomid larvae and pupae. No fishes were found in the stomachs of white crappies taken in March even though they were mature fish. This may be due to the small number of stomachs examined and also due to the absence of gizzard shad fry or other young fry at this early
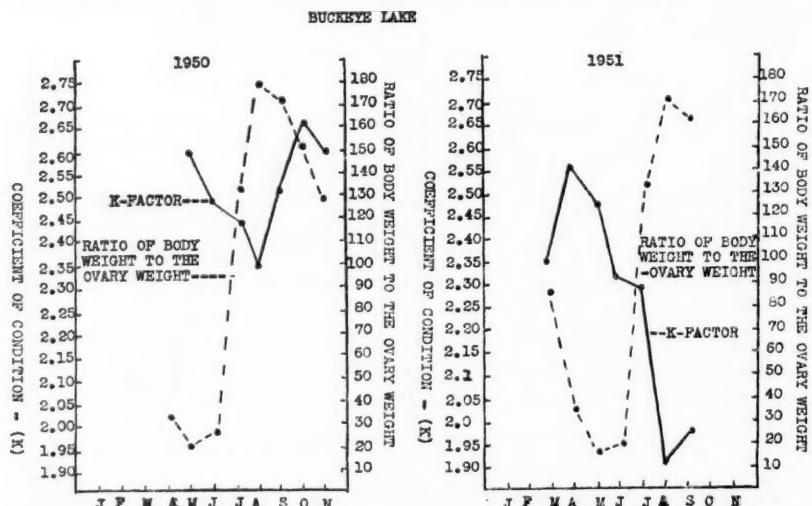
Fig. 10 Relation of coefficient of condition (K) to the body weight–ovary weight ratios

TABLE 7

Food in the Stomachs of 241 White Crappies, Pomoxis annularis (Rafinesque), Taken at the Following Stations: Mud Island, Ayle's Landing, Seller's Point, Miller's Beach, Buckeye Lake Park, Journal Island. Buckeye Lake, Ohio, 1951

	MONTH					
	March	May	June	July	August	Total
	Number of fishes					
	7	96	84	42	42*	273
	per cent	per cent	per cent	per cent	per cent	
Food organisms						
Pisces						
Shad...................		17.5	42.5	78		
Minnow...............		3	1.4			
Sunfish...............			2.4			
Crustacea						
Cladocera.............	21	36	12.6	2.6		
Copepoda.............	79	1	4.5		89.1	
Crayfish..............			1.4			
Insecta						
Chironomidae						
Pupae.................		25.4	24.5	16.5	1.0	
Few larvae...........					9.9	
Corixidae.............				0.3		
Adults...............		0.7	1.5			
Neuroptera						
Sialis larvae..........				2.6		
Unrecognizable..........		16.4	9.2			
Total.....................	100	100.	100.	100.	100.	

* All these fishes were 3 inches or less in total length. The others were between 6 inches and 12 inches in length.

date. The absence of fishes in the stomachs of those taken in August was due probably to their small size, which varied from 2 to 3 inches in length, and the absence of fry small enough to be ingested.

During May, June and July, the ingestion of gizzard shad increased from 17.5% in May to 78% in July. The percentage of crustaceans ingested during these months dropped from 37% in May to 2.6% in July. During March and August, in both large fish and small fish, the ingestion of small crustaceans, primarily cladocera and copepoda, ranged from 100% in March in large fish to 89.1% in August in small crappies. During May, June, and July, chironomid pupae made up an average of 22% of all food eaten by the white crappie. During August chironomid larvae and pupae made up 10.9% of the food eaten by the small fish. However there was a predominance of chironomid larvae over pupae.

This possibly reflects upon the feeding habit of the small fish and large fish. The small fish feed near the bottom or in the vegetation where chironomid larvae are most numerous, while the larger fish feed in the middle and upper zones where the pupae are more numerous.

FACTORS INFLUENCING FEEDING

Temperature

Belding (2) and others believe that water temperature is one of the important factors that influence the feeding activities of fishes. As a rule, while high temperatures slows up these activities it is not true of all species of fish. For example, the feeding activities of the trout decrease as the temperature rises into the seven-
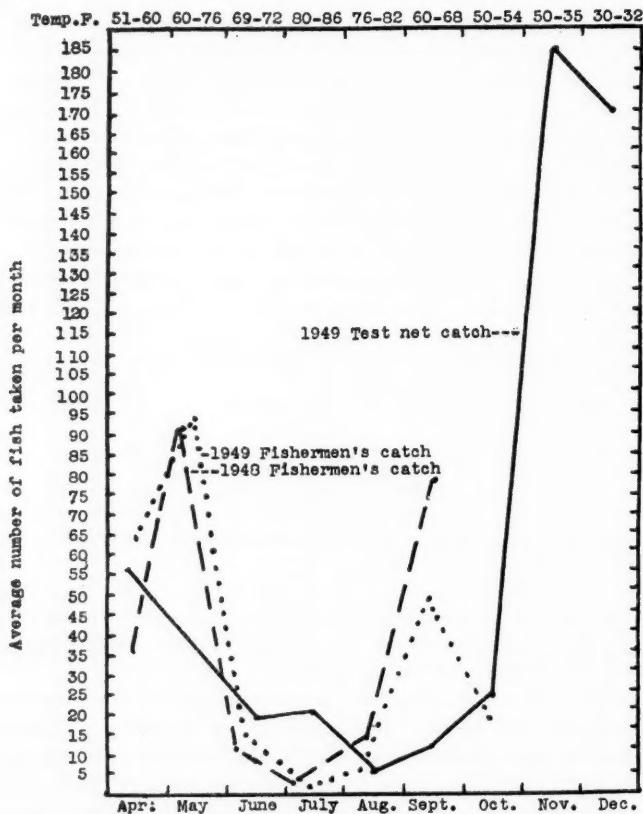
Fig. 11 Average Monthly test net catch for 1949, and average monthly fishermen's catch for 1948 and 1949.

Legend:----Average monthly catch per 100 fishermen for 1948. ———— Average monthly test net catch for each time the net was raised for 1949. ...... Average monthly catch per 100 fishermen for 1949.

ties, while bullheads do not appear to mind temperatures above this. Figure 11 gives the comparison of the average number of white crappies caught per month per 100 fishermen during 1948, and 1949, and the average number of fishes caught in fyke test nets per month for each time the net was raised. Note that these graphs are very similar. From these observations it is assumed that a high test net catch is indicative of increased feeding activities. These periods of activity seem to follow the rise and fall of the temperature. During June, July and the first part of August, when the temperature ranges between 70° and 87° Fahrenheit, both the fishermen's catch and the test net catch are low. Following this, as the temperature begins to drop in late August and in September, both the fishermen's catch and the test net catch increase. Hanson (8) states that at Lake Decatur, Ill., fishermen reported that they caught white crappies principally from March 1 to June 1, and that mid summer fishing was a waste of time. However, in 1953 crappies continued to bite well into mid July.

Light

Light and the time of day may also affect the feeding activities of the white crappie. Figure 12 shows the results of test net catches during intervals of 4 hours for $3\frac{1}{2}$ days. However, it is realized that this is too short a period of study for any conclusive data. The graph (Fig. 12) show definite peaks of activity and inactivity at certain hours of the day and night. On July 13, 14, and 15 peaks of activity occur at 5 A.M., also, on July 13 and 14 at 9 P.M. During the latter days the lowest activity was at 9 A.M.

Spawning

There also seems to be a relation between the spawning period and the feeding activities. During the last of April, May, and early June, when the fish are
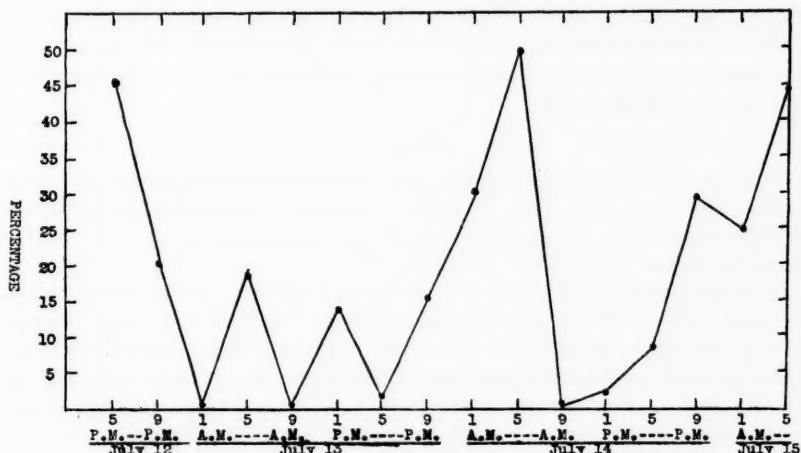
FIG. 12 Percentage of white crappies in the test net at intervals of 4 hours

spawning, the test net catch and fishermen's catch, show increased activity. This is especially true during May when the peak of the spawning period occurs. As the spawning period tapers off in June, there is a drop in both the fishermen's catch and the test net catch (Fig. 11).

Bait

White crappies may be caught by a variety of bait. Live minnows are favorite lures though some fishermen claim that a strip of freshly caught fish measuring little over an inch with the skin retained and placed half an inch below a gold plated spinner is as good as a live minnow. Some fishermen have had excellent results with bass plugs, worms, and artificial bait such as pfluger pilot flies, pfluger pippin wobbler, arbogast tin liz, and others. Usually during spring the best fishing is in shallow water. Later during May and June more crappies are taken in water about 6 feet deep, especially along a boat dock or wharf. When the weather is hot they may be caught with minnows in deeper water. In fishing for crappies the minnow should be moved constantly up and down and sidewise through the water. Very likely places are around brush and snags.

PARASITES AND DISEASE

White crappies of Buckeye Lake are not as high parasitized as the bluegills. Of the 20 white crappies examined by Bangham (1) only 7 were parasitized. Of the 39 bluegills examined 34 were parasitized.

Of the infected white crappies, one was parasitized by the gill fluke belonging to the family Gyradactylidae, and one fish by 4 Cryptogonimas chyli (Osborn). One fish had 2 immature hookheaded worms, Leptorhynchoides thecatus (Linton), and one fish was parasitized by an adult of this form. One fish had one leech and one fish was parasitized by the copepod, Ergasilus caeruleus (Wilson).

In some regions the white crappie may be infected by a virus disease, Lymphocytis. This disease is characterized by white granular shaped masses of enlarged connective tissue cells that appear on the body and on the fins. The disease is not considered fatal, but may cause a stunting of the fins due to a deterioration of the distal end of the finrays.

SUMMARY

This paper is the result of a study of the white crappies of Buckeye Lake, Ohio, during the years 1950, 1951, and 1952, and from information gathered from test net reports,, creel census reports, and from the personnel of the Fish Management Section of the Division of Wildlife, Ohio.

1. White crappies are one of the most abundant of the sunfish family and are common all over the state in our large reservoirs, lakes, and streams. They are easy to propagate and thrive in fairly warm water in shallow lakes and reservoirs.

2. The most active feeding periods of this fish are April, May, and June, and during September and October. The most inactive months are July and August when the water temperatures range between 70° and 87° Fahrenheit.

3. Buckeye Lake white crappies do not mature until they are two years old

and some do not mature until they are three years old. The smallest ripe female observed in Buckeye Lake was 5⅞ inches in length.

4. They begin to spawn during late April and continue to spawn through May, June, and even into July. The height of the spawning period is May and early June. The nesting site is quite variable. They may nest in depths ranging from 2 inches to several feet, and according to one observer to a depth of 20 feet. The nests may be made on mud, sand, clay, gravel, or in vegetation.

5. The number of eggs produced varies from 1908 in fishes 5⅞ in length to 325,677 in fishes 13 inches in length.

6. The incubation period varies between 24 and 27½ hours at temperatures of 70° to 74° Fahrenheit. At hatching they are poorly developed and are capable of very little movement. The head is still attached to the yolk sac. The egg membrane at hatching dissolves into an elastic sticky mass to which the young larvae become stuck head on. The length of the larvae at hatching varies from 1.215 mm. to 1.98 mm. as compared with 2.79 for the bluegill. At 14 days the larvae measured 6 millimeters.

7. The annulus may be formed over a period of several months, from March to September. Young fishes appear to form annuli early in the summer while older fishes form annuli later in the summer.

8. The yearly increment for the first year is greater than in other succeeding years. Following the first year's growth there is a gradual decrease in the yearly increment during each ensuing year with the exception of the fourth and seventh years.

9. The average yearly growth of both male and female is about the same. However during the sixth and seventh years the females grow faster than the males.

10. The plumpness, or K value, of Buckeye Lake white crappies is less than the white crappies of Lake Decatur, Ill., with the exception of fishes 10 and 11 inches in length. As a rule the K values are greater in large fishes than in small fishes.

11. There is a definite relationship between the K values and the ratios of body weight to ovary weight. During the spawning period when the ratios of body weight to ovary weight are low the K values are high.

12. The predominant food of the white crappie is the gizzard shad, followed by midge pupae and Cladocera. During March, Copepods and Cladocera made up 100 % of the food in the stomachs. The food during May consisted of Cladocera, midge pupae, and shad respectively. During June and July the number of midge pupae and Cladocera decreased. In August 89 % of the food eaten consisted of Cladocera. The latter fishes were only three inches and below in length.

13. There is a close relationship between the creel census and the test net catches which indicates the feeding activities of the white crappie. They are most active during March, April, May and June, September and October. During July and August the creel census and test net catches are low and represent the most inactive periods of the summer.

14. The time of the day and night when they are most active is between 5 P.M. and 5 A.M. as shown by the test net catches.

15. Buckeye Lake white crappies are not as highly parasitized as are the bluegills. Only 35% of the white crappies were parasitized as compared with 89% of the bluegills.

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PREFRONTAL LOBOTOMY
AND
ANXIETY REDUCTION IN THE WHITE RAT*

JACK M. STREB

THE PROBLEM

For some time the frontal lobes of the brain have held a particular fascination for physiological psychologists. Unlike many other areas of the brain, the frontal lobes have no clear-cut function. This fact has made them frequent candidates for all sorts of hypothetical speculation. As Carpenter states the problem:

> The frontal lobes of the cerebral cortex are uniquely interesting for two reasons: (a) there is apparently no known, well-defined function which can be attributed to these areas; (b) it is usually assumed that the higher functions, the "symbolic processes" are localized somewhere; because the frontal areas are among the areas without direct sensorimotor connection, they are the logical candidates.
>
> (2, p. 413)

The literature reveals a vigorous program of experimentation involving these little-understood areas of the brain. There have been attempts to localize memory, foresight, and expectancy in the frontal lobes. Another frequent association deals with the relation between the frontal lobes and so-called "anxiety" behavior.

Jacobson (13), Lichtenstein (17), and others have noted a reduction of anxiety in apes and dogs following extirpation of the frontal lobes. The medical team of Freeman and Watts has performed thousands of prefrontal lobotomies on humans to achieve similar results.

The experiment described in this paper will move down the phylogenetic scale to the rat. Using procedures similar to those utilized on higher animals, an attempt has been made to determine whether prefrontal lobotomy is effective in reducing anxiety in the white rat.

APPARATUS

To satisfy the conditions of anxiety defined as a conditioned form of pain, a commercial electric escape apparatus was used. Three main units comprised the experimental equipment: the escape box proper, a control panel, and an electric buzzer.

The escape box consisted of a wooden box 22½" long, 6⅜" wide, and 17½" high. A sliding glass door permitted an animal to be introduced into the box, and

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* This paper was presented in partial fulfillment of the requirements for graduation with honors in Psychology at Denison University in June, 1953.

also served as a means for observing the behavior of the animal. The floor consisted of a steel grid through which an electric shock could be delivered. Projecting through one wall was a spoked drum, arranged so that it could be turned by the rat. Turning the wheel activated a microswitch which turned off any current flowing through the grid floor.

A control panel provided the necessary means for regulating the current and buzzer. A step rheostat made it possible to deliver from 0 to 460 volts through the grid; an AC voltmeter on the panel indicated the strength of the current. The buzzer was plugged into a 6-volt outlet in the back of the panel, and could be sounded by means of a push-button.

Twenty albino rats served as subjects, ten serving as control and ten as experimental animals. They were all males 125–150 days old.

EXPERIMENTAL PROCEDURE

A widely accepted view of anxiety defines it as ". . . a conditioned form of the pain reaction" (20, p. 17). In other words it is a learned anticipatory response to a painful stimulus. This definition of anxiety has the advantage of being non-mentalistic, and amenable to an objective experimental treatment. The concept is based on the work of Mowrer, Miller, Dollard, and others (20, 22). Such an approach also agrees with the characteristics assigned to anxiety by Estes and Skinner:

> Anxiety has at least two defining characteristics: (1) it is an emotional state somewhat resembling fear; (2) the disturbing stimulus which is primarily responsible does not precede or accompany the state, but is "anticipated" in the future.
> (6, p. 390)

The experimental procedure used is shown graphically in Table 1.

The procedure may be described under the headings of original learning, surgery, testing for anxiety reduction, relearning, and post-mortem examination.

Original Learning. Each animal was put into the escape box for a 15 minute period of orientation. At the end of that time learning trials were begun. The buzzer sounded for 5 seconds; then simultaneously the buzzer stopped and a shock of 80 volts was sent through the grid floor of the escape box. During his agitated reaction to the shock, the rat invariably turned the wheel and discontinued the shock. This sequence of buzzer, shock, and wheel-turning constituted one trial. Trials were repeated at 30 second intervals until the rat turned the wheel three consecutive times *during the 5 second period of unreinforced buzzer*. This was

TABLE 1
Experimental Design
Experimental Group

Original Learning	Anesthesia and lobotomy	Test for anxiety reduction	Relearning

Control Group

Original learning	Anesthesia	Test for anxiety reduction	Relearning

taken as the criterion for anxiety. Since an action which was originally elicited only by pain now takes place in the absence of pain, conditioning has taken place. The conditions which define anxiety as a conditioned form of pain have been satisfied.

Surgery. Upon meeting the criterion for anxiety, each of the ten experimental animals was subjected to a prefrontal lobotomy.

Test for Anxiety Reduction. Forty-eight hours following the operation (or the anesthesia in the case of the anesthetized but unoperated control rats) each animal was tested for the retention of his anxiety by returning him to the escape box. The buzzer was sounded for 5 seconds, *but not reinforced by subsequent shock.* Five such trials were given at 30-second intervals for each rat. It was theorized that if the animal had retained its anxiety, such anxiety would be manifested by wheel-turning at the sound of the buzzer. Failure to turn the wheel was interpreted as a reduction in anxiety. Each animal was marked as a "turner" or a "non-turner" for each of his 5 trials.

Relearning. Immediately following the test for anxiety reduction, each animal was re-taught anxiety in exactly the same manner as described under *Original Learning.*

Post Mortem. The ten experimental rats were sacrificed following relearning. Their brains were carefully removed to determine the extent and location of the operative lesions. Brain damage was plotted on diagrams of the rat brain. (See figure 1.)

RESULTS

Originally it was planned to draw conclusions about the anxiety-reducing effect of lobotomy on the basis of data gathered from the Test for Anxiety Reduction. It was thought that testing for significant differences between the number of turns made by experimental as compared with control rats would provide the necessary information for making these conclusions. As can be seen in Table 3, however, there was only one case of wheel-turning out of a possible 50 among the control rats; and there were only two cases out of a possible 50 in the experimental group. Obviously there was no significant difference between the two groups.

Both groups were compared on the number of relearning trials required. Table 2 seems to indicate that significantly more trials were required for relearning by the operated group. A statistical analysis revealed that the experimental and controls animals were not even comparable on the basis of their original learning trials, so no conclusions could be drawn by comparing relearning trials. Nor would any conclusions based on such significance be completely justified, since animals E6 and E7 never did meet the criterion for relearning, but were arbitrarily stopped at 50 trials when it became apparent that no relearning was taking place. Postmortem examination of the brains of these two animals revealed extensive motor damage (Figure 1) which helps to account for this failure to relearn.

The means and standard deviations for the original learning and relearning trials of both groups are shown in Table 2.

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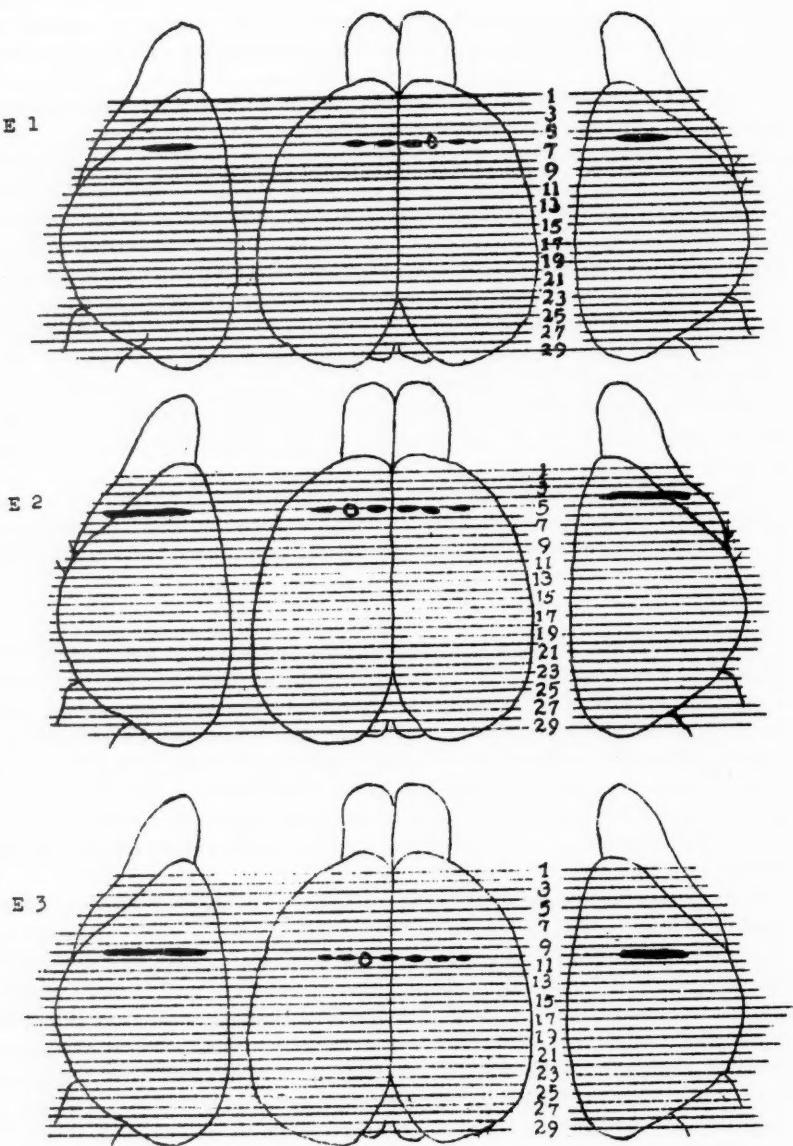
Fig. 1. Brain diagrams showing the extent of lesions
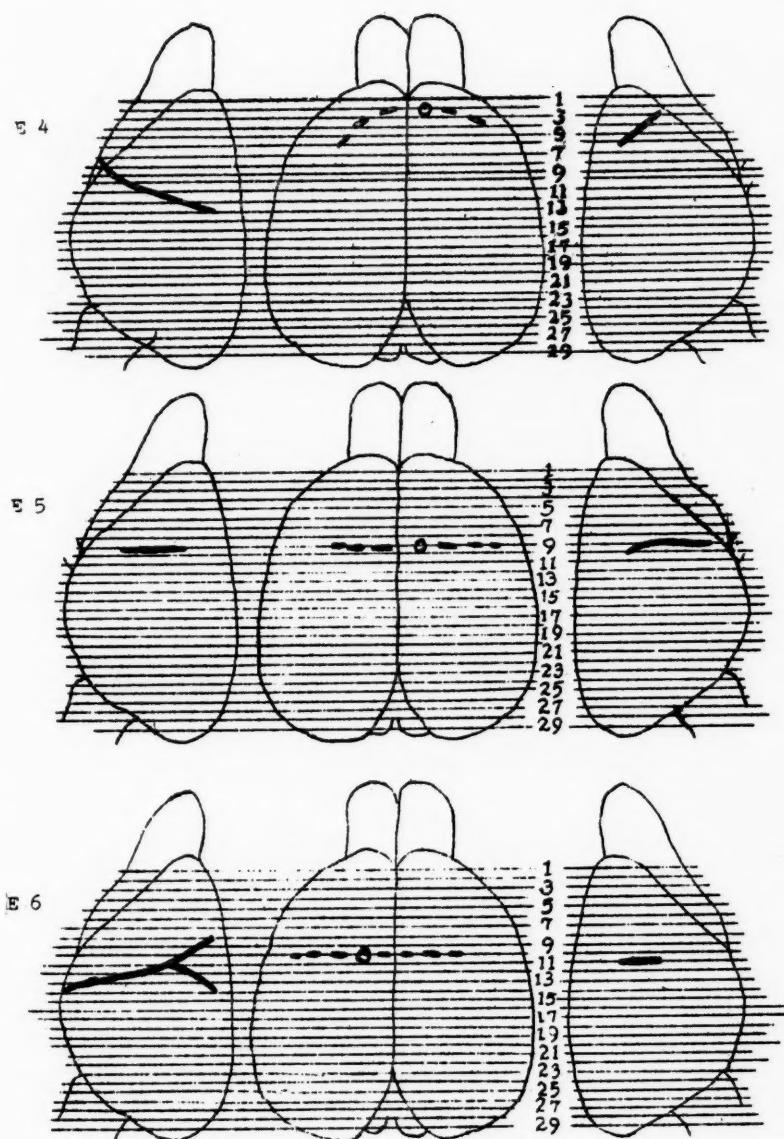
FIG. 1. *Continued*
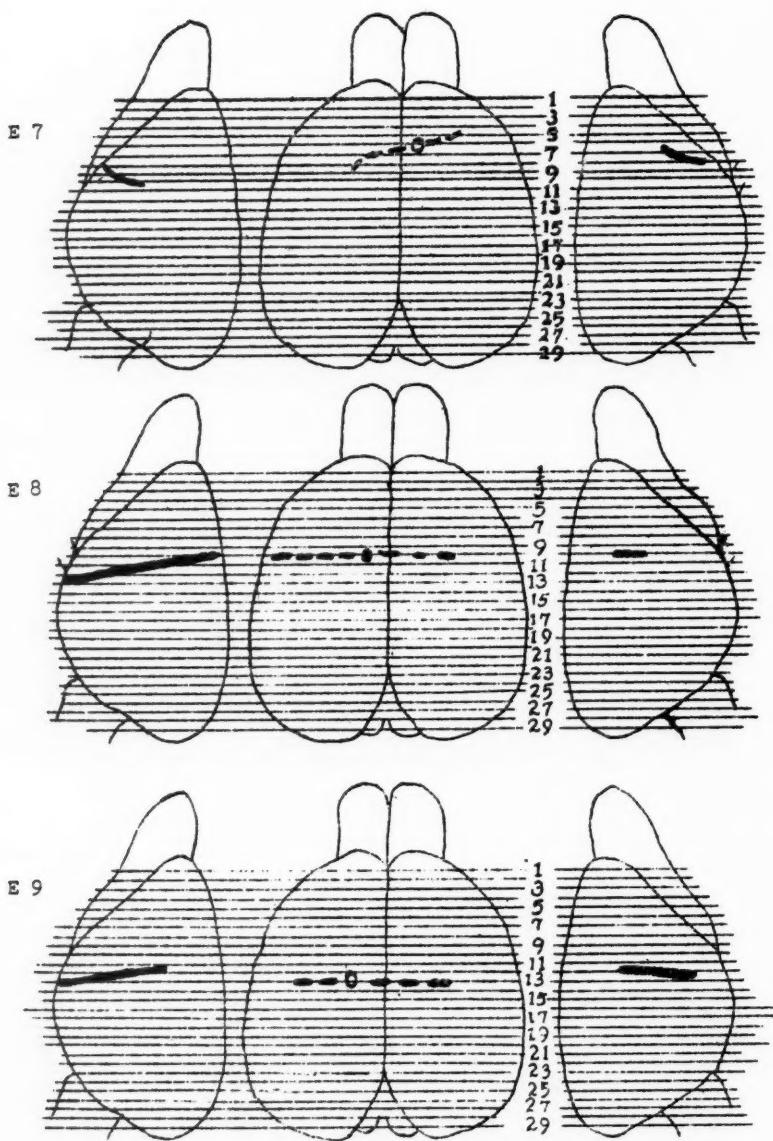
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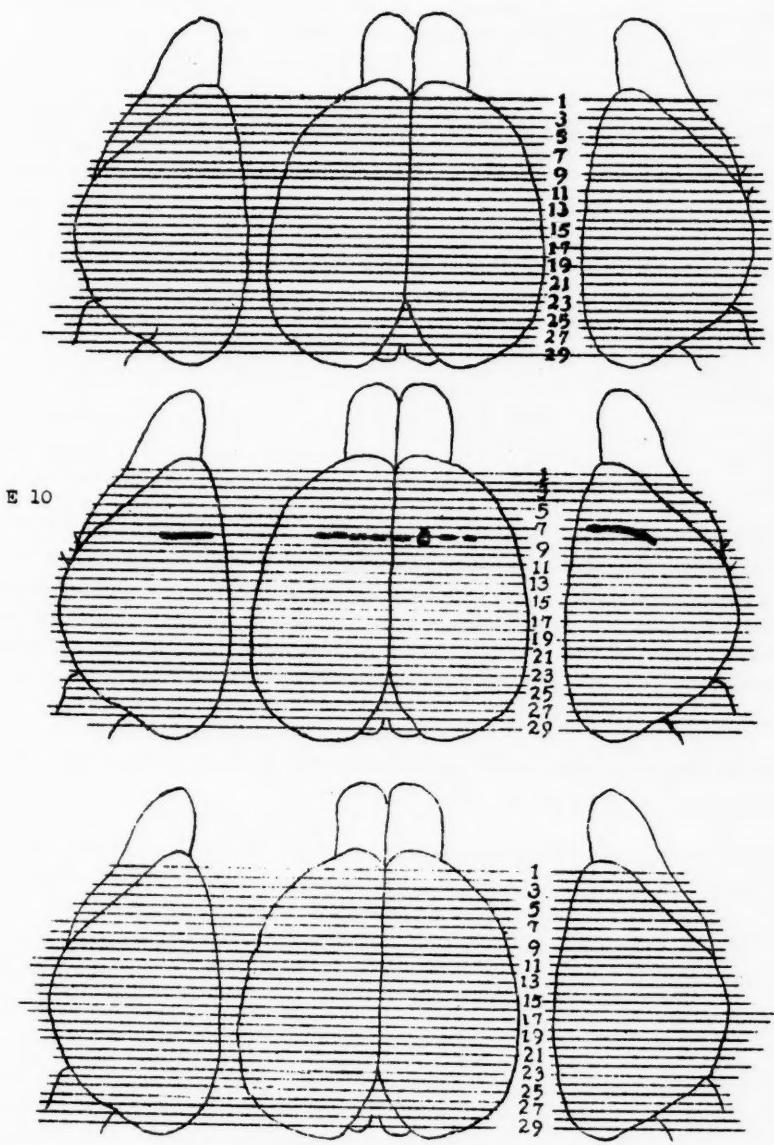
FIG. 1. *Concluded*

TABLE 2

Number of Trials Required to Meet the Criterion; Means and Standard Deviations (in Trials)
for the Experimental and Control Groups

RAT	CONTROL		EXPERIMENTAL	
	Original learning	Relearning	Original learning	Relearning
1	19	5	32	16
2	9	17	14	35
3	6	4	96	43
4	6	14	9	6
5	6	5	9	14
6	16	4	9	50
7	5	8	6	50
8	6	8	4	3
9	9	13	11	30
10	35	8	21	4
$\overline{X}$..................	11.7	8.6	21.1	25.1
SD.................	8.9	4.3	26.1	14.7

In the absence of any conclusive quantitative results, the study must neces-
sarily rely on the qualitative observations recorded during the experiment.

If behavior like greater apparent fear of the experimenter, reluctance to re-
enter the escape box, grooming, and defecation can be interpreted as indicating
anxiety, then the experimental animals showed greater anxiety after surgery
than the control rats. This behavior may have its roots in the operation itself,

TABLE 3

Test for Anxiety Reduction; — indicates no wheel-turning (no anxiety); pos indicates wheel-
turning (anxiety)

TRIAL	RAT NUMBER									
	1	2	3	4	5	6	7	8	9	10
Experimental										
1	—	—	—	—	—	—	—	—	—	—
2	—	—	—	—	—	—	—	—	—	—
3	—	—	pos	—	—	—	—	pos	—	—
4	—	—	—	—	—	—	—	—	—	—
5	—	—	—	—	—	—	—	—	—	—
Control										
1	—	—	—	—	pos	—	—	—	—	—
2	—	—	—	—	—	—	—	—	—	—
3	—	—	—	—	—	—	—	—	—	—
4	—	—	—	—	—	—	—	—	—	—
5	—	—	—	—	—	—	—	—	—	—

which was a painful experience involving extensive neural damage, loss of blood, and probably considerable post-operative pain.

During original learning trials all animals were observed to attack the apparatus, biting the wheel and clawing at the bars making up the grid floor. This behavior was not seen in the experimental rats during reconditioning. During original learning trials the rats tended to turn the wheel "preventively," i.e., almost constantly, as if to prevent further shock through constant manipulation of the wheel. This activity was not seen in the postoperative animals. Instead, they tended to stand by the wheel during the 30 second interim period, become tense (with ears folded back) during the buzzer, and then to turn off the shock as soon as it began. There was no anticipation in the sense that the rat acted to prevent the painful stimulus. In anthropomorphic terms, they seemed content to turn off the shock as soon as it began, but not to prevent it by turning the wheel when the buzzer sounded.

DISCUSSION

Two conclusions can be drawn tentatively from these results. First, lobotomy does not seem to reduce anxiety with the same effectiveness in rats as in phylogenetically higher animals. Or, the results may simply indicate that rats fail to retain anxiety for a period of 48 hours, a conclusion that seems justified on the basis of the dearth of anxiety found in the control group.

Most studies have reported anxiety reduction to be one effect of prefrontal lobotomy (8, 9, 10, 17, 19). Since this paper does not support those results, it might be profitable to examine some of the possibilities underlying the present findings.

Examination of the brain damage charts (Figure 1) indicates that in no case was a complete bilateral prefrontal lobotomy performed successfully. It can be seen that damage is usually unilaterally extensive, with smaller lesions on one side of the brain than on the other. The literature is unanimous in stating that any changes occurring in the organism following extirpation of one lobe are greatly increased following bilateral extirpation.

The possibility exists that the nembutal used as anesthetic may have been responsible for causing changes in the nervous system. Jane Oppenheimer says with reference to this,

> . . . it is difficult if not impossible to handle animals in experiments except under general anesthesia. One of the facts of which we can be most certain, so far as cerebral function is concerned, is that it may be altered by anesthetic drugs.

(23, p. 96)

SUMMARY

Ten experimental and ten control rats were used to determine the effect of prefrontal lobotomy on anxiety reduction. Anxiety was defined as a conditioned form of pain, and induced through the use of an electric escape apparatus.

The rats were taught anxiety. Each experimental animal was then anesthetized and subjected to prefrontal lobotomy. The control animals were anesthetized in the same manner, but no surgery was performed.

Forty-eight hours following the operation (or the anesthesia in the case of the

control animals) the rats were tested for anxiety reduction, then re-taught anxiety to the original criterion. The experimental rats were sacrificed and the extent of their brain damage plotted on charts of the rat brain.

There was no significant quantitative difference in anxiety retention between the experimental and control groups. Several reasons are adduced to help understand these findings.

CONCLUSIONS

1. Anxiety in rats may be susceptible to rather rapid spontaneous extinction.
2. Lobotomy may not be efficacious in reducing anxiety in white rats.

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SOME PROPERTIES OF PERMUTATIONS ON 0, 1, $\cdots$, $(n-1)$ APPEARING IN A PARTICULAR SYSTEM OF CONGRUENCES MODULO n[1]

RICHARD ALBERT DEAN[2]

When Q is a permutation on 0, 1, $\cdots$, $(n-1)$ and $Q(i)$ denotes the image of i under the permutation Q the system of congruence considered is $Q(t) = Q(t+a) + m$, $t = 0, 1, \cdots, (n-1)$ for a, $m < n$. This paper shows how permutations Q can be constructed for which there exist a pair of values a and m such that the system of congruences is satisfied. When $n = p^b$, p a prime, it is shown that exactly $(p-1)\prod_{i=0}^{p^{b-1}-1} (p^b - i \cdot p)$ such permutations exist.

§1 *Introduction*

In what follows Q and R shall denote permutations on the integers 0, 1, $\cdots$, $(n-1)$. We shall denote the image of i, under the permutation Q (or R), by $Q(i)$ [or $R(i)$], frequently writing $i \to Q(i)$ or $Q: i \to Q(i)$ for "i goes into $Q(i)$ under the permutation Q". We shall denote congruence by ($\equiv$), equality by ($=$). The greatest common divisor, d, of two positive integers, s and t, is denoted by $(s, t) = d$ and $\varphi(s)$ is the Euler φ-function denoting the number of positive integers less than or equal to s and relatively prime to s.

This paper is concerned with certain systems of congruences in which the "unknowns" are images of the "knowns" under the permutations Q and R. The first three lemmas belong to the class of "well-known" results but their proofs are typical of those in this paper. The next four lemmas concern elementary facts from elementary number theory and their proofs are omitted.

LEMMA 1. For n an even integer and any permutation Q on 0, 1, $\cdots$, $(n-1)$, there exist integers i and j such that $i \not\equiv j \pmod{n}$ and

$$i - Q(i) \equiv j - Q(j) \pmod{n}.$$

Proof: Since Q is a permutation,

$$\sum_{i=0}^{n-1} Q(i) = \sum_{i=0}^{n-1} i = \frac{n(n-1)}{2}.$$

Moreover if we suppose that the conclusion of the lemma is false, then the set $[i - Q(i)]$ constitute a complete set of residues mod n. Hence a denial of the conclusion gives

$$\sum_{i=0}^{n-1} [i - Q(i)] \equiv \sum_{k=0}^{n-1} k \equiv \frac{n \cdot (n-1)}{2} \pmod{n}.$$

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Hence we have

$$0 = \sum_{i=0}^{n-1} i - \sum_{i=0}^{n-1} Q(i) = \sum_{i=0}^{n-1} [i - Q(i)] \equiv \frac{n \cdot (n-1)}{2} \ (\text{mod } n)$$

or simply

$$\frac{n \cdot (n-1)}{2} \equiv 0 (\text{mod } n)$$

or

$$n \cdot (n-1) = 2 \cdot m \cdot n \text{ for some } m > 0$$

or

$$(n-1) = 2 \, m$$

or $(n-1)$ is even. However n was supposed even, hence $(n-1)$ must be odd, a contradiction.

LEMMA 2. For n even and any permutation Q on $0, 1, \cdots, (n-1)$ there exist integers i and j such that $i \not\equiv j \ (\text{mod } n)$ and $i + Q(i) \equiv j + Q(j)(\text{mod } n)$.

Proof: If $i \rightarrow Q(i)$ is a permutation, then so is $i \rightarrow R(i) \equiv -Q(i)(\text{mod } n)$. If $i \rightarrow R(i)$ is not a permutation, then for some i and j, $i \not\equiv j(\text{mod } n)$, then $R(i) \equiv R(j)(\text{mod } n)$. Hence $-Q(i) \equiv -Q(j)(\text{mod } n)$ or $Q(i) \equiv Q(j)(\text{mod } n)$ or Q is not a permutation, contrary to hypothesis. Now from lemma 1 there exist integers i and j such that $i \not\equiv j(\text{mod } n)$ and $i - R(i) \equiv j - R(j)(\text{mod } n)$, or $i + Q(i) \equiv j + Q(j)(\text{mod } n)$.

Remark: Lemma 2 can be proved independently of lemma 1 in a fashion analogous to the proof of lemma 1.

LEMMA 3. For n even and Q and R arbitrary permutations and for any integer k, there exist integers i and j such that $i \not\equiv j(\text{mod } n)$ and

[1] $i + Q[R(i) + k] \equiv j + Q[R(j) + k](\text{mod } n)$.

Remark: By the notation $Q[R(i) + k]$ we mean the image, under the permutation Q, of the number $R(i) + k$ reduced mod n to a non-negative residue.

Note that here, i and j are dependent on the k. Later we shall consider the problem of finding an i and j which is independent of the k.

Proof: We assert that for fixed k, $i \rightarrow T(i) \equiv Q[R(i) + k](\text{mod } n)$ is a permutation, whence this lemma follows from lemma 2. Now as i runs through $0, 1, \cdots, (n-1)$, so does $R(i)$, in some order, and so does $R(i) + k$, in some other order, since k is fixed. Hence T is the result of first applying the permutation $R(i) + k$ and then, to that result, applying the permutation Q, so T is a permutation.

LEMMA 4. If $a \equiv b(\text{mod } n)$ and d divides two of the three quantities a, b, n, then d divides the third, and

$$\frac{a}{d} \equiv \frac{b}{d} \left(\text{mod } \frac{n}{d}\right).$$

Moreover $ca \equiv cb(\text{mod } cn)$ for any integer c.

LEMMA 5. If $ac \equiv bc(\text{mod } n)$ and $(c, n) = d$, then $a \equiv b(\text{mod } n/d)$. In particular if $d = 1$, then $a \equiv b(\text{mod } n)$.

LEMMA 6. The numbers $0, a, 2a, \cdots, (n-1)a$, for $0 < a < n$, are all distinct mod n if and only if $(a, n) = 1$.

LEMMA 7. The congruence $xa \equiv b(\text{mod } n)$ has a unique (in the range $0 \leqq x < n$) solution $x \equiv c \, (\text{mod } n)$ if and only if $(a, n) = 1$. Moreover if $(a, n) = 1$ then $(c, n) = 1$ if and only if $(b, n) = 1$.

With these lemmas out of the way, we return to the congruence appearing in lemma 3 and ask a slightly different question. For which permutations Q and R do integers i and j exist such that $i \not\equiv j(\text{mod } n)$ and

[1] $$i + Q[R(i) + k] \equiv j + Q[R(j) + k](\text{mod } n)$$

for all $k = 0, 1, \cdots, (n-1)$? Note that this is really a system of congruences and we seek conditions on the Q and R such that the i and j exist, independent of k, satisfying this system of congruences. Section 2 attempts to answer this question. Certain results (theorems 4 and 5) are obtained for general n and, happily, complete information is obtained (theorem 6) when n is a power of a prime.

§2 *Main Theory*

For our study we first transform [1] into a form in which the permutation R plays a minor role and we see that most of the conditions will be imposed on Q. Let

[2]
$$m \equiv (j - i)(\text{mod } n), \qquad a \equiv R(j) - R(i)(\text{mod } n),$$
$$t \equiv k + R(i)(\text{mod } n),$$

then [1] becomes

[3] $$Q(t) \equiv Q(t + a) + m \, (\text{mod } n)$$

for $t = 0, 1, \cdots, (n-1)$.

We now translate the question at hand to read: For what permutations Q does there exist a pair of values a and m such that [3] is satisfied? Note that for a fixed a, a can be represented by $a \equiv x - y(\text{mod } n)$, $0 \leqq x, y < n$, in n different ways. Now if $R(j) = x$, $R(i) = y$ and only two values of R have been prescribed and thus for fixed x, y there are $(n-2)!$ permutations taking $j \rightarrow x$, $i \rightarrow y$. Hence, for fixed i and j (hence fixed m), there exist $n(n-2)!$ permutations, R, such that $a = R(j) - R(i)$. Hence if we count the number, N, of Q's for which a pair a and m exist satisfying [3], then there will be $Nn(n-2)!$ pairs (Q, R) satisfying [1]. A question which we do not attempt to answer is, how many pairs i and j satisfy [3] for a particular Q and R?

We continue our analysis by making a further transformation. Let t in [3]

take on the values $0, a, 2a, \cdots, (n-1)a$, i.e., $t \equiv sa(\mod n)$ for $s = 0, 1, \cdots, (n-1)$. Then [3] implies

[4] $$Q(sa) \equiv Q(0) - sm(\mod n)$$

for $s = 0, 1, \cdots, (n-1)$.

Let us also note, in observing that [3] implies [4], that, since Q is a permutation, if $0, a, \cdots, (n-1)a$ are distinct mod n so are $0, m, \cdots, (n-1)m$, for otherwise values which are distinct mod n would have images congruent mod n under the permutation Q. Conversely, if $0, m, \cdots (n-1)m$ are distinct mod n, so are $0, a, \cdots, (n-1)a$.

THEOREM 1. If $(a, n) = (m, n) = 1$, then

[4] $$Q(sa) \equiv Q(0) - sm(\mod n), \qquad s = 0, 1, \cdots, (n-1)$$

defines a permutation on $0, 1, \cdots, (n-1)$, when we understand the multiples $[sa]$ are reduced mod n for all values of $Q(0)$. This permutation satisfies

[3] $$Q(t) \equiv Q(t+a) + m(\mod n), \qquad t = 0, 1, \cdots, (n-1).$$

Conversely if $(a, n) = (m, n) = 1$ and the permutation Q satisfies [3], then [4] holds and $0, a, \cdots, (n-1)a$ are distinct mod n.

Proof: Since $(a, n) = 1$, from lemma 6 we know that the set $[sa, s = 0, 1, \cdots, n-1]$ are distinct mod n, hence, reduced mod n, are the integers $0, 1, \cdots, n-1$ in some order. Similarly the set $[sm, s = 0, 1, \cdots, n-1]$ are distinct mod n, hence the set $[Q(0) - sm, s = 0, 1, \cdots, n-1]$ are distinct mod n. Hence [4] does define a permutation on $0, 1, \cdots, n-1$.

To verify that [3] holds, let t be arbitrary. Then there exists a solution to the equation $xa \equiv t(\mod n)$ by lemma 7, since $(a, n) = 1$. Thus from [4]:

$$Q(xa) \equiv Q(0) - xm(\mod n)$$

and

$$Q[(x+1)a] \equiv Q(0) - (x+1)m(\mod n).$$

Hence

$$Q(xa) - Q[(x+1)a] \equiv m(\mod n)$$

or

$$Q(xa) \equiv Q[(x+1)a] + m(\mod n).$$

But $xa = t$ and

$$(x+1)a = xa + a \equiv t + a(\mod n),$$

hence

$$Q(t) \equiv Q(t+a) + m(\mod n).$$

To prove the converse we have noted that [3] implies [4] and lemma 6 insures that $0, a, 2a, \ldots, (n-1)a$ are distinct mod n.

Remark: The permutations Q defined by [4] are precisely those sometimes referred to as *distributive,* i.e., those for which $Q(x + y) = Q(x) + Q(y)(\text{mod } n)$ for all x, y, provided $Q(0) = 0$. The proof is left to the reader. Theorem 1 shows there are exactly $\varphi(n)$ of these.

THEOREM 2. There are exactly $n \cdot \varphi(n)$ distinct permutations Q for which there exist at least one pair of values a and m satisfying $(a, n) = (m, n) = 1$ and the system of congruences [3].

Proof: Theorem 1 shows that if $(a, n) = (m, n) = 1$ then [4] defines a permutation Q satisfying [3] and conversely. It remains to count the permutations Q defined by [4].

Case 1: $a = 1$.

Here $Q(0)$ can be chosen in n ways while m can be chosen in $\varphi(n)$ ways. This gives $n \cdot \varphi(n)$ distinct permutations since, for fixed m, two permutations differ at least in the value $Q(0)$ and, for fixed $Q(0)$, the value of $Q(1) = Q(0) - m$ will be different.

Case 2: $a \neq 1$

We shall show that any permutation defined with this a could have been defined under Case 1. Specifically, let a and m and $Q(0)$ be fixed. Consider the permutation defined by [4]

$$Q(sa) \equiv Q(0) - sm(\text{mod } n), \ s = 0, 1, \ldots, (n - 1).$$

We shall exhibit an m_1 such that the permutation Q_1 defined by $Q_1(0) = Q(0)$ and

$$Q_1(s) \equiv Q(0) - sm_1(\text{mod } n), \ s = 0, 1, \ldots, (n - 1)$$

is equal to Q. Since $(a, n) = 1$, there is an m_1 such that $am_1 \equiv m(\text{mod } n)$. Moreover since $(m, n) = 1$ and $(a, n) = 1$, then $(m_1, n) = 1$, by lemma 7. Now let $sa \equiv x(\text{mod } n)$. It suffices to show that $Q(sa) \equiv Q_1(x)(\text{mod } n)$. Now

$$Q_1(x) \equiv Q(0) - xm_1(\text{mod } n), \text{ by definition,}$$

$$\equiv Q(0) - sam_1(\text{mod } n)$$

$$\equiv Q(0) - sm(\text{mod } n)$$

$$\equiv Q(sa), \text{ by definition.}$$

Hence we have shown that by using an $a = 1$, no more permutations Q can be defined by [4] other than those in Case 1.

We next consider the case that $(m, n) = d > 1$ and we prove a lemma generalizing the observation made in the paragraph just preceding theorem 1.

LEMMA 8. If Q is a permutation and a and m are values for which [3] holds, then $(a, n) = (m, n)$.

Proof: When $(a, n) = 1$ or $(m, n) = 1$, we have already shown that $(a, n) = 1 = (m, n)$. Hence suppose that $(m, n) = d > 1$. Hence $m = dh$, $n = dg$ and $(g, h) = 1$. We first show that $0, m, 2m, \ldots, (g - 1)m$ are distinct (mod n). Suppose $sm \equiv tm(\text{mod } n)$ for $0 \leqq s, t < g$. Then by lemma 4 $sh \equiv th(\text{mod } g)$ and now, as $(h, g) = 1$ by lemma 5, $s \equiv t(\text{mod } g)$. But this last is impossible on the range of s and t unless $s = t$.

Now since [3] implies the validity of [4] and since $[Q(0) - sm, s = 0, \ldots, (g - 1)m]$ are distinct mod n and Q is a permutation, then $0, a, \ldots, (g - 1)a$ are distinct (mod n). But moreover,

$$Q(ga) = Q(0) - gm = Q(0) - gdh = Q(0) - nh.$$

Hence

$$Q(ga) \equiv Q(0)(\text{mod } n).$$

Hence

$$ga \equiv 0(\text{mod } n)$$

or

$$ga = un = udg \qquad\qquad \text{for some } u > 0.$$

Upon cancelling the g we see that d divides a. Since d also divides n, d divides (a, n).

Repeating the argument, beginning with $(a, n) = d'$ we find that d' divides (m, n). Hence $d = d'$.

Notation: We shall use as standard for the remainder of the paper the following notation:

$$(a, n) = (m, n) = d, \qquad n = dg, \qquad m = dh, \qquad a = dk.$$

Note that $(g, h) = (g, k) = 1$.

Now we may take [4] as defining the permutation Q for the values $0, a, \ldots, (g - 1)a$ reduced mod n. To complete the definition of Q we first prove a lemma describing a display of all the residues mod n.

LEMMA 9. Let $(a, n) = (m, n) = d, n = dg, m = dh, a = dk$.
The following display of $n = dg$ numbers are all distinct mod n.

0	a	$2a$	$\cdots$	$(g - 1)a$
1	$a + 1$	$2a + 1$	$\cdots$	$(g - 1)a + 1$
2	$a + 2$	$2a + 2$	$\cdots$	$(g - 1)a + 2$
.	.	.		.
.	.	.	$\cdots$	.
.	.	.		.
$(d - 1)$	$a + (d - 1)$	$2a + (d - 1)$	$\cdots$	$(g - 1)a + (d - 1)$.

[5]

Proof: Consider the congruence

$$sa + p \equiv ta + q \pmod{n}$$

$$\text{where } 0 \leqq s, t < g; 0 \leqq p, q < d.$$

Hence

$$(s - t)a \equiv (q - p) \pmod{n}.$$

From lemma 4, d must divide $(q - p)$ since d divides a and n. But this is impossible on the range of p and q unless $p = q$. Then dividing out the d we have

$$(s - t)k \equiv 0 \pmod{g}.$$

But since $(k, g) = 1$, lemma 5 tells us $s \equiv t \pmod{g}$, which again is impossible on the range of s and t unless $s = t$.

We wish to use [5] to define a permutation Q which will satisfy [3] for some a and m, where $(m, n) = d > 1$. To this end we define

[6] $$Q(sa + p) \equiv Q(p) - sm \pmod{n},$$

$$\text{where } 0 \leqq s < g; 0 \leqq p < d,$$

and where $Q(0), Q(1), \ldots, Q(d - 1)$ are subject only to the condition:

[7] $$\text{If } 0 \leqq p < q < d, Q(q) \not\equiv Q(p) - tm \pmod{n}$$

for $0 \leqq t < g$.

LEMMA 10. The definition [6], with respect to [7], is a permutation on $0, 1, \ldots, (n - 1)$, where we understand that the $[sa + p]$ are reduced mod n.

Proof: Lemma 9 has shown the set $[sa + p]$ of $0 \leqq s, t < g; 0 \leqq p, q < d$ to be distinct mod n. Hence [6] defines a value for every residue mod n. To show that [6] is a permutation consider the congruence

$$Q(ta + q) \equiv Q(sa + p) \pmod{n},$$

where s, t, p and q are in the prescribed ranges. Hence from definition [6] we are really considering

$$Q(q) - tm \equiv Q(p) - sm \pmod{n}.$$

It suffices to show that $ta + q \equiv sa + p \pmod{n}$.

Now suppose $p = q$. Then our congruence becomes $tm \equiv sm \pmod{n}$ or by lemma 5 $t \equiv s \pmod{g}$, but this is impossible on the range of s and t unless $s = t$. Hence $ta + q = sa + p$. If however $q \not\equiv p$ and, let us assume $p < q$, then the hypothesis

$$Q(ta + q) \equiv Q(sa + p) \pmod{n}$$

now yields

$$Q(q) \equiv Q(p) - (s - t)m \pmod{n}.$$

It will be shown that this implies

$$Q(q) \equiv Q(p) - rm(\text{mod } n)0 \leqq r < g,$$

contrary to condition [7], and thus $p \not< q$. Take $r \equiv (s - t)(\text{mod } g)$ and $0 \leqq r < g$. Then, by lemma 4,

$$rd \equiv (s - b)\, d(\text{mod } gd) \text{ or } (\text{mod } n).$$

Thus

$$rdh \equiv (s - t)\, dh(\text{mod } n)$$

or

$$rm \equiv (s - t)m(\text{mod } n)$$

and we have exhibited the necessary r. Similarly $q \not< p$ and we conclude that $p = q$.

THEOREM 3. If $(a, n) = (m, n) = d$, then a permutation is defined by [6] for any choice of $Q(0), Q(1), \ldots, Q(d - 1)$ subject only to condition [7], and it satisfies

[3] $$Q(t) \equiv Q(t + a) + m(\text{mod } n)\ t = 0, 1, \ldots, (n - 1).$$

Conversely if $(a, n) = (m, n) = d$ and the permutation Q satisfies [3], then [6] holds and condition [7] is satisfied.

Proof: Lemma 10 has shown that a permutation is defined in this way. Now let t be arbitrary,
let

$$t \equiv sa + p(\text{mod } n),$$

then

$$(t + a) \equiv (s + 1)a + p(\text{mod } n).$$

Case 1. $(s + 1) < g$.
Then by definition

$$Q(t) \equiv Q(sa + p) \equiv Q(p) - sm(\text{mod } n)$$

while

$$Q(t + a) \equiv Q(p) - (s + 1)m(\text{mod } n).$$

Hence

$$Q(t + a) + m \equiv Q(p) - (s + 1)m + m$$
$$\equiv Q(p) - sm$$
$$\equiv Q(sa + p)$$
$$\equiv Q(t)(\text{mod } n).$$

Case 2. $(s + 1) = g$.
Then

$$(t + a) \equiv (s + 1)a + p \equiv ga + p \equiv p(\text{mod } n),$$

since

$$ga = g \cdot d \cdot k = n \cdot k \equiv 0(\text{mod } n).$$

Hence

$$Q(t + a) + m \equiv Q(p) + m \equiv Q(p) - sm \equiv Q(t)(\text{mod } n)$$

provided we can show $-sm \equiv m(\text{mod } n)$, or $(s + 1)m \equiv 0(\text{mod } n)$. To that end:

$$(s + 1)m = gm = g \cdot d \cdot h = hn \equiv 0(\text{mod } n).$$

To prove the converse of theorem 3, let $t = p$. Then [3] says $Q(p) \equiv Q(p + a) + m(\text{mod } n)$. Now let

$$t = p, p + a, p + 2a, \ldots p + (n - 1)a,$$

and as in deriving [4], [3] yields

$$Q(sa + p) \equiv Q(p) - sm(\text{mod } n), \qquad s = 0, 1, \ldots, (n - 1).$$

Hence [6] holds. Now suppose [7] is violated. Then

$$Q(q) \equiv Q(p) - tm(\text{mod } n) \qquad \text{for } 0 \leq p < q < d$$

and $0 \leq t < g$. Now, since [6] holds, we have

$$Q(ta + p) \equiv Q(p) - tm(\text{mod } n).$$

Hence

$$Q(q) \equiv Q(ta + p)(\text{mod } n)$$

and, since Q is assumed to be a permutation, we must have $q \equiv ta + p(\text{mod } n)$. But this is impossible for the range of p, q and t in view of lemma 9.

THEOREM 4. The number of permutations Q for which there exists a pair of values, a and m, satisfying [3] when $(a, n) = (m, n) = d > 1$ and $a = dk$, $n = dg$ is given by

[8] $$\varphi(g) \cdot \prod_{j=0}^{i=d-1} (n - i \cdot g).$$

Proof: From theorem 3 it is clear we need only count how many distinct permutations Q can be defined by [6], obeying condition [7] with all possible pairs a, m. Initially let a pair a, m by chosen and fixed. From [6] and [7] it is clear we have only to prescribe the values of $Q(0), Q(1), \ldots, Q(d - 1)$. For a choice of $Q(p)$, $0 \leq p < d$, $(g - 1)$ more values of Q are given by [7]. Thus at the beginning there are n values possible for $Q(0)$. For $Q(1)$, then, there are

$$n - g = n - \frac{n}{d}$$

choices. For $Q(2)$,

$$n - g - g = n - 2g = n - \frac{2 \cdot n}{d}$$

choices, and so on, until finally for $Q(d - 1)$ there are

$$n - (d - 1)g = n - \frac{(d - 1)n}{d}$$

choices. Hence, for fixed a and m, $\prod_{i=0}^{d-1} (n - i \cdot g)$ permutations are defined by [6], all of which satisfy condition [7].

Now let us keep m fixed, but select another value "a", calling it a_1, subject to the restriction that $(a_1, n) = d$. Let $a_1 = dk_1$, hence $(k_1, g) = 1$. We prove:

LEMMA 11. The permutation Q defined by [6], satisfying [7] with respect to a and m, is distinct from the permutation Q_1 defined by [6], satisfying [7] with respect to a and m, subject to the condition $(a, n) = (a_1, n) = (m, n) = d$, where $a = dk$, $a_1 = dk_1$ if $k \not\equiv k_1 (\bmod\ g)$. Conversely, if $k \equiv k_1 (\bmod\ g)$ and $Q(p) = Q_1(p)$ for $0 \leqq p < d$, then the permutations Q and Q_1 are identical.

Proof: First let us suppose that $k \not\equiv k_1 (\bmod\ g)$. We note that if $x \equiv sa + p \equiv ta_1 + q (\bmod\ n)$ where $0 \leqq s, t < g, 0 \leqq p, q < d$, then $p = q$ and t satisfies $sk \equiv tk_1 (\bmod\ g)$. This is so since $sa + p \equiv ta_1 + q (\bmod\ n)$ implies $(sa - ta_1) \equiv q - p (\bmod\ n)$ and d divides n and $sa - ta_1$, hence d divides $q - p$ by lemma 4. But this is possible on the range of p and q only if $p = q$. Hence we have $sa \equiv ta_1 (\bmod\ n)$ and again from lemma 4 $sk \equiv tk_1 (\bmod\ g)$.

We shall show that $Q_1 = Q$ by showing that for $x \equiv a + p \equiv ta_1 + p (\bmod\ n)$, $0 \leqq p < d$ then $Q(x) \not\equiv Q_1(x) (\bmod\ n)$. Now since $a + p \equiv ta_1 + p (\bmod\ n)$ we know t satisfies $k \equiv tk_1 (\bmod\ g)$. Now

$$Q(a + p) \equiv Q(p) - m (\bmod\ n)$$

and

$$Q_1(ta + p) \equiv Q_1(p) - tm (\bmod\ n)$$

by definition. If Q is to be equal to Q_1 certainly $Q(p) \equiv Q_1(p) (\bmod\ n)$. Here $Q(a + p) \equiv Q_1(ta_1 + p) (\bmod\ n)$ implies $m \equiv tm (\bmod\ n)$ or $1 \equiv t (\bmod\ g)$, by lemma 5. But $k \equiv tk_1 (\bmod\ g)$, hence $k \equiv k_1 (\bmod\ g)$, contrary to hypothesis.

Conversely suppose $k \equiv k_1 (\bmod\ g)$ and

$$Q(p) \equiv Q_1(p) (\bmod\ n) \qquad\qquad \text{for } 0 \leqq p < d.$$

Let

$$x \equiv sa + p \equiv ta_1 + q (\bmod\ n).$$

As before $p \equiv q$ and $sa \equiv ta_1 (\bmod\ n)$ and t satisfies $sk \equiv tk_1 (\bmod\ g)$. We must show $Q(x) \equiv Q_1(x) (\bmod\ n)$, or that

$$Q(sa + p) \equiv Q(p) - sm \equiv Q_1(p) - tm \equiv Q_1(ta_1 + p) (\bmod\ n).$$

It suffices to show $sm \equiv tm \pmod{n}$. Since $sk \equiv tk_1 \pmod{g}$ and $k \equiv k_1 \pmod{g}$, we have $sk = tk_1 \equiv tk \pmod{g}$. Since $(k_1 g) = 1$, by lemma 5 we have $s \equiv t \pmod{g}$. Hence $sd \equiv td \pmod{gd}$ or $sd \equiv td \pmod{n}$; hence $sdh \equiv tdh \pmod{n}$ or $sm \equiv tm \pmod{n}$.

Hence the proof of the lemma is complete. We now count the number of positive k's which are incongruent, mod g, in pairs and all of which satisfy $(k, g) = 1$. We may restrict ourselves to k's which are less than or equal to g, since we are using them to form $a = dk$ and $a \leq n$. All positive k's less than or equal to g satisfy the condition that they be incongruent, mod g, in pairs. The restriction $(k, g) = 1$ still remains and so there are exactly $\varphi(g)$ such k's. Hence with fixed m, the number of distinct permutations Q defined by [6], satisfying [7] is given by

$$\varphi(g) \prod_{i=0}^{d-1} (n - i \cdot g).$$

The next lemma shows that no new permutations can be defined by changing the value m.

LEMMA 12. Given a_1, m, m_1 such that $(a_1, n) = (m, n) = (m_1, n) = d$, $m = dh$, $m_1 = dh_1$, $a_1 = k_1 d$, and a permutation Q_1 defined by [6] and satisfying [7] with respect to a_1 and m_1, there exists a value a such that $(a, n) = d$ and a permutation Q defined by [6], satisfying [7] with respect to a and m such that Q is identical with Q_1.

Proof: First let x be a solution to

$$xh \equiv h_1 \pmod{g}.$$

Lemma 7 assures a solution exists and that $(x, g) = (h_1, g) = 1$ since $(h, g) = 1$. Now take k as the unique solution to $xk = k_1 \pmod{g}$. Lemma 7 again does the trick assuring also that $(k, g) = 1$. Now take $a = kd$. We shall show that this works. Clearly $(a, n) = d$ since $(k, g) = 1$. We shall now define Q.

First, define $Q(p) = Q_1(p)$ for $0 \leq p < d$.

Second, note that, as in the proof of lemma 11,

$$sa + p \equiv ta_1 + q \pmod{n} \text{ and } 0 \leq p, q < d$$

implies $p = q$ since $(a, n) = (a_1, n) = d$.

Now consider

$$x \equiv sa + p \equiv ta_1 + p \pmod{n}.$$

We shall show that under definition [6]

$$Q(sa + p) \equiv Q(p) - sm \equiv Q_1(p) - tm_1 \equiv Q_1(ta_1 + p) \pmod{n}.$$

Since $Q(p)$ is defined equal to $Q_1(p)$, it suffices to show $sm \equiv tm_1 \pmod{n}$. From $sa \equiv ta_1 \pmod{n}$ we conclude

$$sk \equiv tk_1 \pmod{g},$$

by lemma 4. Recall that $xk \equiv k_1 (\mathrm{mod}\ g)$ and $xh \equiv h_1 (\mathrm{mod}\ g)$. Hence

$$shk_1 \equiv shxk \equiv sh_1 k \equiv skh_1 \equiv tk_1 h_1 \equiv th_1 k_1 (\mathrm{mod}\ g).$$

But $(k_1, g) = 1$, hence

$$sh \equiv th_1 (\mathrm{mod}\ g)$$

and

$$shd \equiv th_1 (\mathrm{mod}\ gd),$$

by lemma 4, or

$$sm \equiv tm_1 (\mathrm{mod}\ n).$$

Furthermore Q satisfies condition [7] since, if it does not, this implies, by what has just been shown, that Q_1 does not.

This completes the proof of lemma 12 and hence theorem 4.

THEOREM 5. Let m_1 and m_2 be such that $(n, m_1) = d_1$ and $(m_2, n) = d_2$ and $d_2 = ed_1$, i.e., d_1 divides d_2. Let $(a_1, n) = d_1$ and let Q_1 be any permutation defined by [6], satisfying [7] with respect to m_1 and a_1. Then there exists a value a_2 and a permutation Q_2 defined by [6], satisfying [7] with respect to m_2 and a_2, such that $Q_1 = Q_2$.

Notation: $m_1 = h_1 d_1$, $m_2 = h_2 d_2$, $n = d_1 g_1 = d_2 g_2 = ed_1 g_2$, $a_1 = k_1 d_1$. With this notation $(k_1, g_1) = 1$, $(h_1, g_1) = 1$, $(h_2, g_2) = 1$.

LEMMA 13. $(e, h_1) = 1$, $(h_1, g_2) = 1$, $(h_2 k_1, g_2) = 1$.

Proof: We note from $n = d_1 g_1 = d_2 g_2 = ed_1 g_2$ that $g_1 = eg_2$. Now suppose f divides e. Then f divides g_1. If g also divides h_1, then f divides $(g_1, h_1) = 1$. Thus $f = 1$ and the only common divisor of e and h_1 is 1.

Next any divisor of g_2 is a divisor of g_1, hence any divisor of g_2 and h_1 is a divisor of g_1 and h_1. The only divisor of this pair is 1, hence $(g_2, h_1) = 1$.

Finally any prime f dividing $h_2 k_1$ and g_2 must divide k_2, as $(h_2, g_2) = 1$. But any number dividing g_2 must also divide g_1, hence f must divide g_1 and k_1. But $(g_1, k_1) = 1$ so f must be 1 hence $(h_2, k_1, g_2) = 1$.

Proof of Theorem 5: We begin by defining $Q_2(0), Q_2(1), Q_2(2), \ldots, Q_2(d_1 - 1)$ by

$$Q_2(p) = Q_1(p) \qquad\qquad \text{for } 0 \leqq p < d_1.$$

To define $Q_2(q)$ for $d_1 \leqq q < d_2$, take q and write

$$q \equiv sa_1 + p (\mathrm{mod}\ n) \quad 0 \leqq s < g_1, 0 \leqq p < d_1.$$

This can be done uniquely since [5] showed that all residues mod n, in particular q, appear once and only once in [5]. Then define

$$Q_2(p) \equiv Q_1(sa_1 + p) \equiv Q_1(p) - sm_1 (\mathrm{mod}\ n)$$

$$\equiv Q_2(p) - sm_1 (\mathrm{mod}\ n).$$

We remark, moreover, that if we take $p \equiv q \pmod{d_1}$ and $0 \leq p < d_1$ and select the s such that

$$sk_1 = \frac{q - p}{d_1} \pmod{g_1}$$

(such an s exists as d_1 divides $q - p$ by the choice of p while $(k_1, g_1) = 1$), then $q \equiv sa_1 + p \pmod{n}$. For

$$sk_1 \equiv \frac{q - p}{d_1} \pmod{g_1}$$

implies

$$sk_1 d_1 \equiv q - p \pmod{g_2 d_1},$$

by lemma 4, or

$$sa_1 + p \equiv q \pmod{n}.$$

Hence we may conclude that

$$q \equiv sa_1 + p \pmod{n}$$

$$0 \leq s < g_1, \ 0 \leq p < d \text{ if and only if } p \equiv q \pmod{d_1}$$

and

$$sk_1 \equiv \frac{q - p}{d_1} \pmod{g_1}.$$

Now these choices for $Q_2(r)$, $0 \leq r < d_2$ enable us to use definition [6]. We must show that condition [7] is satisfied and that $Q_1 = Q_2$. We show that condition [7] is satisfied for any a_2 such that $(a_2, n) = d_2$. We shall later specify the value of a_2 to be used.

Suppose that [7] does not hold, i.e.,

$$Q_2(q) \equiv Q_2(s) - wm_2 \pmod{n}$$

for $0 \leq w < g_2$ and $0 \leq s < q < d_2$ for some s, q and w. By definition:

$$Q_2(s) \equiv Q_1(t) - lm_1 \pmod{n}$$

where

$$s \equiv t \pmod{d_1} \quad \text{and} \quad lk_1 \equiv \frac{s - t}{d_1} \pmod{g_1}$$

and

$$Q_2(q) \equiv Q_1(p) - rm_1 \pmod{n}$$

where

$$p \equiv q \pmod{d_1} \quad \text{and} \quad rk_1 \equiv \frac{q - p}{d_1} \pmod{g_1}.$$

Consequently the denial of condition [7] yields:

[9] $Q_1(p) - rm_1 \equiv Q_2(q) \equiv Q_1(t) - lm_1 - wm_2(\text{mod } n).$

Case 1. $p = t.$
Here [9] yields

$$-rm_1 \equiv -lm_1 - wm_2(\text{mod } n)$$

or

$$(l - r)m_1 \equiv -wm_2(\text{mod } n)$$

or

$$(l - r)h_1 \equiv -wh_2e(\text{mod } eg_2)$$

by lemma 4, and we see now that e must divide $(l - r)h_1$. By **lemma 13** $(e, h_1) = 1$ so e must divide $(l - r)$. Now from

$$lk_1 = \frac{s - t}{d_1} (\text{mod } g_1)$$

and

$$rk_1 = \frac{q - p}{d_1} (\text{mod } g)$$

and $p = t$, we have

$$(l - r)k_1 \equiv \frac{s - q}{d_1} (\text{mod } g_1).$$

Now since e divided $(l - r)$ and e divides g_1, we conclude by **lemma 4** that e divides $(s - q)/d_1$ or that $ed_1 = d_2$ divides $s - q$. But this contradicts the hypothesis $0 \leq s < q < d_2$.

Case 2. $t < p.$
Here [9] yields

$$Q_1(p) \equiv Q_1(t) - [(l - r)m_1 + wm_2](\text{mod } n).$$

Now if a v can be produced such that

$$(l - r)m_1 + wm_2 \equiv vm_1(\text{mod } n), \qquad\qquad 0 \leq v < g_1$$

then we shall have $Q_1(p) \equiv Q_1(t) - vm_1(\text{mod } n)$. To produce the v:
First choose x such that

$$xh_1 \equiv -wh_2e(\text{mod } g_1).$$

Since $(h_1, g_1) = 1$, this can be done. Then choose

$$v \equiv (l - r) - x(\text{mod } g_1).$$

Thus $0 \leq v < g_1$ is immediately satisfied. Now consider:

$$(l - r - v)h_1 + wh_2e \equiv 0(\bmod\ g_1)$$

and thus

$$(l - r - v)h_1d_1 + wh_2ed_1 \equiv 0(\bmod\ g_1d_1)$$

or

$$(l - r)m_1 - vm_1 + wm_2 \equiv 0(\bmod\ n)$$

or

$$vm_1 \equiv (l - r)m_1 + wm_2(\bmod\ n),$$

as was to be shown.

Case 3. $t > p$.

A proof similar to case 2 shows a similar contradiction.

To complete the proof of theorem 5 we must show how to choose a_2 so that $Q_2 = Q_1$ on the remainder of the residues mod n.

First let k_2 be such that

$$k_2h_1 \equiv h_2k_1(\bmod\ g_2).$$

Such a k_2 exists since $(h_1, g_2) = 1$ by lemma 13. Then define $a_2 = k_2d_2$. We want to show that this works. At least $(a_2, n) = d_2$ since $(k_2, g_2) = 1$. This is so since $(h_2k_1, g_2) = 1$ as was shown in lemma 13. Lemma 7 then applies.

To summarize the proof so far, we are trying to find a value, a_2, and values of $Q_2(r)$ $0 \leq r < d_2$ such that when Q_2 is completely defined by [6], condition [7] is satisfied and $Q_2 = Q_1$. We have chosen the values of Q_2 so that they agree with Q_1 for $0 \leq r < d_2$. Moreover we have shown that with this beginning, condition [7] is satisfied with any a_2, just so $(a_2, n) = d_2$. Then we have picked from a hat, so to speak, a value a_2 which satisfies $(a_2, n) = d_2$. We do know at this point that Q_2 is a permutation. We want to show that for any residue $x = 0, 1, \ldots,$ or $(n - 1)$, $Q_2(x) \equiv Q_1(x)(\bmod\ n)$. We proceed as follows:

Consider $Q_2(sa_2 + p)$. By definition

$$Q_2(sa_2 + p) \equiv Q_2(p) - sm_2 \equiv Q_1(u) - wm_1 - sm_2(\bmod\ n)$$

for $P \equiv u(\bmod\ d_1)$ and $wk_1 \equiv (p - u)/d_1\ (\bmod\ g_1)$. Now we show that there exists a v such that $vm_1 \equiv wm_1 + sm_2(\bmod\ n)$. Since $(h_1, g_1) = 1$, we may take an f such that

$$fh_1 \equiv sh_2e(\bmod\ g_1)$$

from which it follows, by lemma 4,

$$fm_1 \equiv sm_2(\bmod\ n).$$

Then $v \equiv f + w(\bmod\ g_1)$ gives

$$vm_1 \equiv vh_1d_1 \equiv wm_1 + fm_1 \equiv wm_1 + sm_2(\bmod\ n).$$

Hence

$$Q_2(sa_2 + p) \equiv Q_1(u) - vm_1 (\text{mod } n)$$
$$\equiv Q_1(va_1 + u)(\text{mod } n).$$

The latter congruence follows from the definition of Q_1.

Since Q_2 and Q_1 are both permutations, it follows that the $va_1 + u$ such that $Q_2(sa_2 + p) \equiv Q(va_1 + u)(\text{mod } n)$ is unique. It then suffices to show that

$$sa_2 + p \equiv va_1 + u(\text{mod } n).$$

From the definition of a_2 we have

$$k_2 h_1 \equiv h_2 k_1 (\text{mod } g_2)$$

and hence

$$k_2 h_1 e \equiv h_2 k_1 e(\text{mod } g_2 e)$$

and

$$sk_2 h_1 e \equiv sh_2 k_1 e(\text{mod } g_1) \text{ since } g_1 = eg_2,$$
$$\equiv fh_1 k_1 (\text{mod } g_1)$$

since $(h_1, g_1) = 1$, then

$$sk_2 e \equiv fk_1 (\text{mod } g_1).$$

Hence

$$sk_2 e + \frac{p - u}{d_1} \equiv fk_1 + \frac{p - u}{d_1} \ (\text{mod } g_1)$$
$$\equiv fk_1 + wk_1 \equiv (f + w)k_1 (\text{mod } g_1)$$
$$\equiv vk_1 (\text{mod } g_1).$$

Hence

$$sk_2 ed_1 + p - u \equiv vk_1 d_1 (\text{mod } g_1 d_1)$$

or

$$sa_2 + p - u \equiv va_1 (\text{mod } n)$$

or

$$sa_2 + p \equiv va_1 + u(\text{mod } n)$$

and the proof of theorem 5 is finally complete.

Corollary 5.1: Let $(m_1, n) = (a_1, n) = 1$. Let Q_1 be defined as in Theorem 1. Let $(m_2, n) = d_2 > 1$. Then there exists a value a_2 and a permutation Q_2 defined by [6], satisfying [7] with respect to m_2 and a_2 such that $Q_2 = Q_1$.

Proof: The proof of theorem 5 goes through in this case with the modification that $d_1 = 1$ and all congruences mod d_1 are to be regarded as bona-fide equalities.

The reader may find it informative to complete the details of this proof or to give an independent one.

THEOREM 6: If n is the power of a prime p, $n = p^b$, then the number of permutations Q on $0, 1, \ldots, (n - 1)$ for which there exist values a and m satisfying [3] is exactly

$$(p - 1)\prod_{k=0}^{p^{b-1}-1} (p^b - kp).$$

Proof: For any $m < n = p^b$, either $(m, n) = 1$ or $(m, n) = p^c$ where $c < b$. Theorem 5 and corollary 5.1 show that all permutations defined by [6] and [7] may be found by considering those thus defined with an m such that $(m, n) = p^{b-1}$, the largest possible greatest common divisor of any m and n. Theorem 4 tells us that in this case, $(m = p^{b-1}, d = p^{b-1}, g = p)$ the number is

$$\varphi(p)\prod_{i=0}^{p^{b-1}-1} (p^b - i\cdot p) = (p - 1)\prod_{i=0}^{p^{b-1}-1} (p^b - i\cdot p).$$

§3 *Conclusion*

Left unanswered by these theorems are the questions about permutations defined by [6] and [7] in cases where $(m_1, n) = d_1$ and $(m_2, n) = d_2$ but d_2 is not a multiple of d_1 or vice versa. The two sets of permutations will certainly overlap since, from corollary 5.1 and theorem 2, they both contain the permutations generated by an m such that $(m, n) = 1$ and $a = 1$. Examples can be constructed in which the "overlap" is even greater.

Dr. Burton V. Dean has indicated the following theorem and its proof to the author.

THEOREM 7. (B. V. Dean) There are $n^2\cdot\varphi(n)$ pairs of permutations Q, R on $0, 1, \ldots, (n - 1)$ such that

[1] $$i + Q[R(i) + k] = j + Q[R(j) + k](\bmod n)$$

for all i, j, k.

Proof: Let us assume that [1] holds for all i, j, and k. In particular let k take on the values $\equiv -R(i)$, mod n. Then [1] reads

[10] $$i + Q(0) = j + Q[R(j) - R(i)](\bmod n)$$

for all i and j. Here let i be such that $R(i) = 0$, hence $R^{-1}(0) = i$. Then [10] reads

[11] $$R^{-1}(0) + Q(0) \equiv j + Q[R(j)](\bmod n)$$

for all j. Similarly let j be such that $R(j) = 0$, or $j = R^{-1}(0)$ in [10]. Hence

[12] $$i + Q(0) \equiv R^{-1}(0) + Q[-R(i)](\bmod n)$$

for all i. Combining [11] and [12] we obtain

[13] $$(i - j) + 2Q(0) \equiv Q[R(j)] + Q[-R(i)](\bmod n)$$

for all i and j. Now from [10] we have

[14] $(i - j) + Q(0) \equiv Q[R(j) - R(i)](\text{mod } n)$

or, combining [13] and [14],

$$Q[R(j) - R(i)] + Q(0) \equiv Q[R(j)] + Q[-R(i)](\text{mod } n)$$

or

[15] $Q[R(j) + (-R(i))] + Q(0) \equiv Q[R(j)] + Q[-R(i)](\text{mod } n)$

for all i and j, hence for all $R(j)$, $-R(i)$, hence for all a and b,

[16] $Q(a + b) + Q(0) \equiv Q(a) + Q(b)(\text{mod } n).$

Thus [16] is a necessary condition for [1] to hold for all $i, j,$ and k.

A second necessary condition, [18], is derived as follows: Let $k = 0$ in [1]. Then

[17] $i + QR(i) \equiv j + QR(j)(\text{mod } n)$

for all i and j. Let i_0 be such that $QR(i_0) = 0$, then

$$i_0 \equiv j + QR(j)(\text{mod } n),$$

or

[18] $QR(j) \equiv i_0 - j(\text{mod } n)$

for all j.

Moreover conditions [16] and [18] are sufficient for [1] to hold for all i, j and k. We may interpret [18] as defining the permutation QR for arbitrary i_0. Hence we have for arbitrary i and j,

[19] $QR(j) \equiv i_0 - j(\text{mod } n)$

and

$$QR(i) \equiv i_0 - i(\text{mod } n)$$

or

$$QR(j) - QR(i) \equiv i - j(\text{mod } n)$$

or

$$i + QR(i) \equiv j + QR(j)(\text{mod } n)$$

or, for arbitrary k,

$$i + QR(i) + Q(k) - Q(0) \equiv j + QR(j) + Q(k) - Q(0)(\text{mod } n)$$

or, using [16],

$$i + Q[R(i) + k] \equiv j + Q[R(j) + k](\text{mod } n),$$

which was to be shown.

It remains to count the number of pairs Q, R where Q satisfies [16] and QR satisfies [18]. Let P be a distributive permutation, one such that

$$P(a + b) \equiv P(a) + P(b)(\mathrm{mod}\ n).$$

Then it is asserted that any permutation Q defined by

[20] $$Q(i) \equiv m + P(i)(\mathrm{mod}\ n)$$

satisfies [16].

Now $P(0) \equiv 0(\mathrm{mod}\ n)$ by the remark preceding theorem 2, and hence $Q(0) \equiv m(\mathrm{mod}\ n)$. Hence, computing $Q(a + b)$, we have

$$Q(a + b) \equiv m + P(a + b)(\mathrm{mod}\ n)$$
$$\equiv m + P(a) + P(b)(\mathrm{mod}\ n)$$

or

$$Q(a + b) + m \equiv P(a) + m + P(b) + m(\mathrm{mod}\ n)$$

or

$$Q(a + b) + Q(0) \equiv Q(a) + Q(b)(\mathrm{mod}\ n).$$

Conversely if Q has property [16] then $P(i) \equiv Q(i) - m(\mathrm{mod}\ n)$ defines a distributive permutation. Now from the remark just referred to and the proof of theorem 1 we find there are just $\varphi(n)$ permutations P, thus $n \cdot \varphi(n)$ permutations Q can be defined by [20], hence just that many Q's satisfy [16].

Next, from condition [18] we see

$$R(j) \equiv Q^{-1}(i_0 - j)(\mathrm{mod}\ n)$$

and there are n values for i_0. Since once i_0 is chosen and Q is chosen, R is uniquely determined. So the number of pairs will be

$$n \cdot n \cdot \varphi(n), \text{ or } n^2 \cdot \varphi(n).$$